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SCIENTIFIC PUBLICATIONS

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COVER IMAGE

Following the devastating earthquake and fire that engulfed San Francisco and the Academy on 18 April 1906, the Academy found temporary quarters to house what little it had rescued from the ruins of its once proud Market Street museum. Its library, once the largest natural history library in the United States west of Saint Louis had, like nearly all of its biological collections, disappeared in the conflagration. Although the significance of the loss of the library can never be fully appreciated, there came such an outpouring of generosity from institutions and individuals worldwide that its library soon regained much of its former luster. The post-earthquake library, which is shown in the cover illustration, was housed in a large Gough Street home, which itself had come through the events of 18 April relatively unscathed. The names of institutions, individuals, and, yes, even book dealers, who opened up their inventories, at no cost to the struggling Academy, were duly recorded in the early recovery-period records of the institution and on bookplates that were affixed to the books received (see also Leviton & Aldrich, *Theodore Henry Hittell's The California Academy of Sciences, 1853–1906*. California Academy of Sciences, San Francisco, 1997, pp. 561–563).

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"Cephalaspidean" Heterobranchs (Gastropoda) from the Pacific Coast of Costa Rica

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Based on phylogenetic evidence, Mikkelsen (1996) demonstrated that the traditional taxon "Cephalaspidea" is paraphyletic. As a consequence of this new phylogenetic hypothesis, the Acteonidae, Bullinidae, and Ringiculidae were removed from the traditional Cephalaspidea. Furthermore, the Acteonidae was removed from the Opisthobranchia and included in an unresolved group named "Lower Heterobranchia." The Bullinidae and Ringiculidae remained in the Opisthobranchia, but were included in another unresolved group, the "Architectibranchia." After the exclusion of these taxa, the rest of the Cephalaspidea remained as a monophyletic group. Members of the paraphyletic traditional Cephalaspidea are here referred to as "cephalaspidean" heterobranchs. Despite the fact that "cephalaspidean" heterobranchs are paraphyletic, it is still practical to deal with them in monographic treatises due to morphological similarities (presence of large, external shells in most groups), shared habitats and life modes, and consistency with historical treatments.

Little is know about the "cephalaspidean" heterobranch biodiversity in Costa Rica. Studies by Houbrick (1968), Robinson and Montoya (1987), Høisæter, (1998), and more recently by Espinosa and Ortea (2001), provided a few records from the Caribbean and Pacific coast, but included no morphological comparisons for most taxa.

The purpose of the present study is to provide an up-to-date catalogue of species of "Lower Heterobranchia," "Architectibranchia," and Cephalaspidea found along the Pacific coast of Costa Rica, including descriptions of a new species and a systematic review of the generic placement and synonymy of several other species previously described, based on new anatomical evidence.

Material and Methods

All specimens studied, including the type material, are deposited at the Instituto Nacional de Biodiversidad, Costa Rica (abbreviated INB), the Natural History Museum of Los Angeles County (abbreviated LACM), the California Academy of Sciences, San Francisco (abbreviated CASIZ), The Natural History Museum, London (abbreviated BMNH), and the National Museum of Natural History, Washington D.C. (abbreviated USNM). The material examined is labeled as "shell" for dried shells (with or without remaining tissue), and "specimen" for complete wet specimens including shell and soft parts. Taxa have been arranged according to a classification system based on the phylogenetic hypothesis by Mikkelsen (1996).

All wet specimens available were dissected and morphological examination was facilitated by

breaking the shell. The internal features were examined and drawn using a dissecting microscope with a camera lucida. Dried shells with remaining tissue were re-hydrated and broken to dissect the radula and other hard parts. The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried, and mounted for examination with a Scanning Electron Microscope (SEM). Gizzard plates were dissected and mounted for examination with a SEM.

Species Descriptions

"Lower Heterobranchia"

Family Acteonidae d'Orbigny, 1843

Genus *Acteon* de Monfort, 1810

***Acteon traskii* Stearns, 1897**
(Figs. 1A–D)

Acteon traskii Stearns, 1897:14.

Type material.— *Acteon traskii*: Holotype: Spanish Bight, San Diego, California (USNM 2506).

Material examined.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 1 shell (CASIZ 170722). 1 mile offshore, between Bahía Elena and Bahía San Juanillo (10°57′20″N, 85°46′08″W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-12.43). From 1.75 miles west of Punta Descarte to 1.25 miles north of start, off Bahía Santa Elena (11°02′23″N, 85°48′05″W), Provincia Guanacaste, 55 m depth, 14 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-15.15). 5 miles north west of Islas Huevos (10°41′45″N, 85°46′25″W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-34.25). Middle of Bahía Huevos, north of Bahía Culebra (10°38′41″N, 85°41′55″W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-35.39). Off beach at Bahía Ballena (9°44′12″N, 84°59′32″W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-45.37). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 1 juvenile shell, leg. J. McLean (LACM 72-54.50). Isla David (10°57′51.5100N, 85°42′36.9080W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 39 m depth, 2 March 1996, 3 shells, leg. Y. Camacho (INB0003747064). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 1 shell, leg. Y. Camacho (INB0003747061). 800 meters from Isla Despensa, Murciélago (10°59′45.3350N, 85°44′16.2441W), Provincia Guanacaste, 40 m depth, 9 April 2002, 1 shell, leg. F. González (INB0003539758).

Additional material examined.— Mexico: Bahía Chamela, Jalisco, 27–72 m depth, 1 shell, 16 February 1938, leg. G. Willett (LACM 153410). Bahía Tangola-Tangola and Bahía Santa Cruz (15°45′00″N, 96°06′12″W), Oaxaca, 18–37 m depth, 28 February 1934, 2 shells with body parts (LACM 34-133.26). Colombia: Bahía Choco (3°33′N, 77°38–39′W), southwest of Buenaventura, 80 m depth, 16 September 1966, 1 shell (LACM 66-201.8).

Shell morphology.— Length 12 mm; width 5 mm, in the largest specimen examined from Costa Rica. Shell solid, elongate, with convex sides (Fig. 1A). Body whorl large, from ¾ to ⅘ of the shell length. Spire short, conical, with 3–4 short whorls. Suture slightly channeled. Protoconch globose, about 1.5 whorl, 500 µm in diameter (Fig. 1B). Umbilicus absent. Aperture long, about ¾ of the body whorl length, wide anteriorly, narrowing abruptly about its half-length. Anterior end of the aperture expanded into a small lip that is more conspicuous near the middle of the shell. Columellar margin thickened, slightly oblique, with a small, simple fold. Sculpture composed of a

number of punctured spiral grooves (Fig. 1D). Punctuations oval, fused to each other within each groove, more conspicuous near the anterior end of the shell. Grooves separated by gaps several times as wide as the grooves. Color cream to reddish, with a white band on the posterior end of the whorl. Some specimens with the reddish pigment faded out or completely disappeared.

ANATOMY.— Radular formula 121 × 133.0.133 in a specimen from Mexico (LACM 34-133.26). Radular teeth all similar in shape and size, with an elongate base and a curved cusp bearing 15–17 elongate denticles (Fig. 1C).

GEOGRAPHIC RANGE.— Recorded from Southern California to Panama (Keen 1971). The present paper includes the first record from Colombia.

REMARKS.— *Acteon traskii* was described based on Holocene material from southern California (Stearns 1897). Living animals have been reported from southern California to Panama (Keen 1971) and Marcus (1972) provided descriptions of the radula and penial anatomy. This species can be distinguished from *Rictaxis punctocaelatus* (Carpenter, 1864) by having a more fragile, reddish shell with a single white band on the posterior end of the whorl. In *R. punctocaelatus* the shell is dark grey to black with three white bands on the anterior end, middle region, and posterior end of the whorl. The radula of *R. punctocaelatus* described by Marcus (1972) contains a much smaller number of teeth, which are larger and vary in shape along the half-row, from short multidenticulate inner teeth to very elongate outer teeth.

Gosliner (1996) studied one specimen from the Santa Barbara Basin (Southern California) with the shell and radular morphology identical to the specimens here examined. It is most likely that Gosliner's material belongs to the same species.

Acteon panamensis Dall, 1908 is a much shorter and fragile species originally described from deep waters in Panama (Dall 1908).

Rudman (1971) proposed that *Acteon* should be used only for species with a columellar fold and numerous minute hook-shaped teeth. Other genus names are available for species with no columellar fold or radulae with a reduced number of teeth. The anatomy of numerous species and genera of Acteonidae has not been described, so it is not possible to determine their generic placement or synonymy.

Acteon traskii is placed in the genus *Acteon* because of the presence of a wide radula with numerous short teeth, similar to that of *Acteon tornatilis* (Linnaeus, 1758), the type species of the genus. For a description of the radula of *A. tornatilis* see Thompson (1976).

Genus *Crenilabium* Cossmann, 1889

Crenilabium venustus (d'Orbigny, 1840)

(Figs. 1E–G)

Acteon venustus d'Orbigny, 1840:399, pl. 56, figs. 4–6.
? *Daphnella casta* Hinds, 1844:25.

TYPE MATERIAL.— *Acteon venustus*: type material untraceable. *Daphnella casta*: HOLOTYPE: Golfo de Nicoya, Costa Rica (BMNH 79.2.26.89).

MATERIAL EXAMINED.— Five miles north west of Islas Huevos (10°41′45″N, 85°46′25″W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 3 shells, 1 fragment, leg. P. LaFollette and D. Cadien (LACM 72-34.26). South of Punta Uvita to Isla Ballena (9°07′36″N, 83°44′30″W), Provincia Puntarenas, 18 m depth, 13 March 1972, 1 fragment, leg. J. McLean (LACM 72-61.22).

ADDITIONAL MATERIAL.— Intertidal drift shells in crab colony, Fort Amador Beach (8°56′N, 79°33′W), Canal Zone, Panama, 14 March 1970, 1 shell, leg. A. Marti (LACM 70-85.1).

SHELL MORPHOLOGY.— Length up to 12 mm; width up to 4 mm in the largest specimen exam-

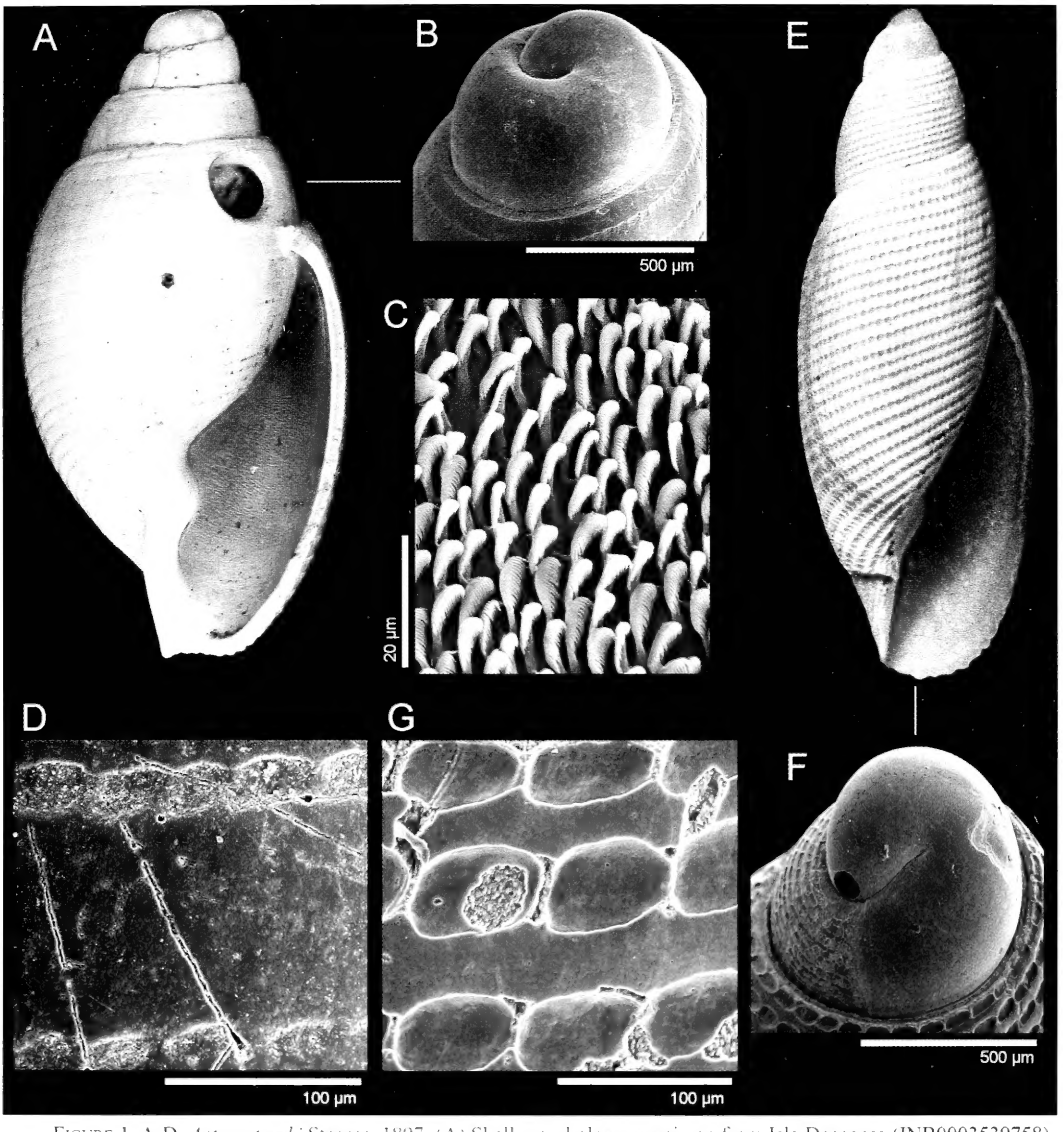

FIGURE 1. A-D, *Acteon traski* Stearns, 1897: (A) Shell morphology, specimen from Isla Despensa (INB0003539758), 6 mm long; (B) Protoconch, specimen from Isla David (INB0003747061); (C) Radular teeth, specimen from Bahia Tangola-Tangola, Mexico (LACM 34-133.26); (D) Sculpture, specimen from Isla David (INB0003747061). E-G, *Crenilabium venustus* (d'Orbigny, 1840): (E) Shell morphology, specimen from Amador Beach, Panama (LACM 70-85.1), 9 mm long; (F) Protoconch, specimen from Punta Uvita (LACM 72-61.22); (G) Sculpture, same specimen.

ined. Shell solid, very elongate (Fig. 1E). Body whorl long, between 4/5–5/6 of the shell length; spire conical, elongate, with 2–3 whorls. Suture narrowly channeled. Protoconch elongate, about 1.5 whorl, 600 µm in diameter (Fig. 1F). Umbilicus absent. Aperture narrow and short, about 3/4 of the body whorl. Columellar margin with a conspicuous denticle. Sculpture composed of a number of punctured spiral grooves (Fig. 1G). Punctuations conspicuous, oval, situated next to each other within each groove. Grooves separated by gaps with about the same width as the grooves. Color uniformly whitish.

Anatomy.— All the specimens examined consisted of empty shell so anatomical examinations were not possible.

Geographic range.— Reported from Costa Rica to Peru (Keen 1971).

Remarks.— *Acteon venustus* d'Orbigny, 1840 was originally described from Paita, Peru (d'Orbigny 1840). This species is characterized by having a narrow and elongate shell, with an elongate spire, a relatively short aperture, and a strong sculpture composed of conspicuous punctuations. There is no information on the anatomy of this species that was described on the basis of empty shells. The material here examined from Costa Rica and Panama matches the original description and it is clear that it belongs to the same species.

Because there are no anatomical data, it is not possible to provide a positive taxonomic placement for this species. Bouchet (1975) provided anatomical and conchological evidence for maintaining the fossil genus *Crenilabrum* as valid, those include a radula with lateral teeth provided with a long and sharp cusp and a rachidian tooth, and a shell with a very elongate spire and comparatively short aperture. The type material of *Acteon venustus*, as well as the specimens here examined, resembles the conchological features of *Crenilabrum*. Thus, this species is here tentatively transferred to *Crenilabrum* until complete specimens become available for study.

Daphnella castus (Hinds, 1844) was originally described as a member of the Turridae, and later transferred to *Acteon* by Keen (1971). The holotype of this species (BMNH 79.2.26.89) is partially broken, but the general outline of the shell is very similar to that of *Crenilabrum venustus* and these two names are most likely synonyms.

Genus *Rictaxis* Dall, 1871

Rictaxis punctocaelatus (Carpenter, 1864)

Tornatella punctocaelata Carpenter, 1864:646.

Remarks.— This species has been reported in the literature from Alaska to Baja California (Keen 1971; Skoglund 2002). The LACM collection holds one lot containing two shells collected alive from Isla San Miguel, Panama (LACM 157893). No specimens have been collected so far from Costa Rica but it is likely that this species is present in this area.

Rictaxis punctocaelatus is characterized by having a solid and elongate shell with a black or dark gray background color and three spiral white bands on the anterior and posterior ends of the spire as well as in the middle region. The radula and external morphology of this species was described by Gosliner (1996).

Opisthobranchia
Cephalaspidea
Family Cylichnidae H. and A. Adams, 1854

Genus *Cylichna* Lovén, 1846

Cylichna atahualpa (Dall, 1908)

(Figs. 2A–C)

Cylichnella atahualpa Dall, 1908:243, pl. 11, fig. 2.

Type material.— *Cylichnella atahualpa*: Holotype: Gulf of Panama (USNM 123081).

Material examined.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 1 shell (CASIZ 170721). Bahía Chatham (5°33′20″N, 86°59′10″W), Cocos Island, 26 m depth, 13 January 1938, 11

shells (LACM 38-179.4). Golfo Dulce (8°24′20″N, 83°13′40″W), Provincia Puntarenas, 35–88 m depth, 26 March 1939, 1 shell (LACM 39-44.23). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57′20″N, 85°46′08″W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 7 shells and fragments, leg. P. LaFollette and D. Cadien (LACM 72-12.45). Half mile to one mile and half west of Roca Vagares, Bahía de San Juanillo (10°57′28″N, 85°45′20″W), Provincia Guanacaste, 37 m depth, 14 February 1972, 2 shells, leg. D. Cadien and P. LaFollette (LACM 72-13.33). Five miles north west of Islas Huevos (10°41′45″N, 85°46′25″W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 10 shells, leg. P. LaFollette and D. Cadien (LACM 72-34.28). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 4 shells, leg. J. McLean (LACM 72-54.52). Off Isla del Caño (8°45′N, 83°54′W), Provincia Puntarenas, 55 m depth, 16–17 March 1972, 6 shells, leg. J. McLean (LACM 72-66.40).

Shell morphology.— Length up to 12 mm; width up to 3 mm in the largest specimen examined. Shell solid, elongate, with nearly parallel sides (Fig. 2A). Only one whorl visible, forming nearly the entire shell. Apex rounded, umbilicated, with the aperture lip rising from the right side. Anterior end of the shell rounded, slightly flattened in some specimens. Aperture as long as the shell, wider anteriorly and narrowing gradually at about ⅕ of its length. Columellar margin conspicuously thickened. Umbilicus absent. Sculpture with a number of irregular spiral lines more conspicuous near the anterior and posterior ends of the shell. Color dirty white, covered with a pale brown or yellowish periostracum. Spiral lines near the anterior and posterior borders of the shell pale brown. Apex and columella opaque white.

Anatomy.— The digestive system contains three smooth gizzard plates similar in shape and size. All the plates are oval and elongate (Fig. 2C). The radular formula is 12 × 4.1.1.1.4 in a specimen from Golfo Dulce (LACM 39-44.23). The rachidian teeth are broad with a number of sharp denticles decreasing in size towards the laterals of each plate. The innermost lateral teeth are hook-shaped, with a long and strong cusp with numerous minute denticles (Fig. 2B). The four outermost teeth of each row are much smaller, but also hook-shaped with a long and thin cusp and several small denticles.

Remarks.— *Cylichna atahualpa* was described based on shells collected at 590 m depth from the Gulf of Panama (Dall 1908). The original description included an illustration of an elongate shell with no umbilicus and the columellar margin conspicuously thickened. The color of the shell was described as white with a pale yellowish periostracum that shows reddish brown in the incised sculpture. The material here examined is from shallower waters but fits the original description and characteristics of the holotype of *Cylichna atahualpa*.

This species was originally described as a member of *Cylichnella*, but the anatomy of the specimens examined, with three oval and smooth gizzard plates, and a radula with several lateral teeth, are typical of species of *Cylichna*.

Other species assigned to *Cylichna*, also described or reported from the Panamic Province, are *Cylichna luticola* (C.B. Adams, 1852), *Cylichna inca* (Dall, 1908), and *Cylichna pizarro* (Dall, 1908). According to the illustrations provided by Keen (1971), these species are proportionally shorter and wider than *C. atahualpa* and lack conspicuous spiral lines on the shell, except for *C. pizarro*.

Cylichna diegensis (Dall, 1919), originally described from San Diego, California, and with a geographic range extending from Santa Monica to Baja California, has a similar shell morphology to *C. atahualpa*. The anatomy of *C. diegensis* was described by Gosliner (1996), and it differs from that of *C. atahualpa* in several regards. The inner lateral teeth of *C. diegensis* bear 9–11 large denticles under the main cusp, whereas in *C. atahualpa* there are numerous minute denticles. Additionally, the outermost teeth of *C. diegensis* are smooth, whereas in *C. atahualpa* they have numerous denticles.

Genus *Acteocina* Gray, 1847

Acteocina infrequens (C.B. Adams, 1852)

(Figs. 2D–H)

Bulla (*Tornatina*) *infrequens* C.B. Adams, 1852:214, 319.
Acteocina magdalenensis Dall, 1919:296.
Acteocina angustior Baker and Hanna, 1927:124–125, pl. 4, fig. 5.

Type material.— *Bulla* (*Tornatina*) *infrequens*: Lectotype: Panama (MCZ 186451). *Acteocina magdalenensis*: Holotype; Bahía Magdalena, Baja California, Mexico, leg. C. R. Orcutt (USNM 218410). *Acteocina angustior*: Holotype: Puerto Escondido, Baja California, Mexico (CASIZ 032116).

Material examined.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 6 shells (CASIZ 170720). Bahía Cocos (10°33′35″N, 85°42′30″W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 31 shells (LACM 33-123.32). Puerto Parker (10°57′50″N, 85°48′45″W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 11 shells (LACM 35-113.27). Bahía Salinas (11°03′33″N, 85°43′47″W), 11 February 1935, 4 shells (LACM 35-117.19). Bahía Salinas (11°03′33″N, 85°44′05″W), 11 February 1935, 1 shell (LACM 35-122.16). Between Punta Isla and 500 m South of Punta Isla (10°56′00″N, 85°48′55″W), Bahía Santa Elena, Provincia Guanacaste, 1–11 m depth, 13 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-7.33). Southeast end of Bahía Santa Elena, approximately half mile offshore (10°55′15″N, 85°48′30″W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, >50 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.18). Bahía Potrero Grande (10°50′56″N, 85°48′35″W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 17 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.12). Middle of Bahía Huevos, north of Bahía Culebra (10°38′41″N, 85°41′55″W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 3 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.44). Off beach at Bahía Brasilito (10°25′57″N, 85°49′18″W), Provincia Guanacaste, 18 m depth, 20 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.35). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 3 shells, leg. J. McLean (LACM 72-54.56). Isla del Caño (8°44′00″N, 83°52′30″W), Provincia Puntarenas, 12 m depth, 14–19 March, 1972, 6 shells, leg. J. McLean (LACM 72-64.18). 250 m off Punta Piedra (8°35′24.6720N, 83°11′26.3250W), Provincia Puntarenas, 23 m depth, 14 April 1997, 2 shells, leg. M. Madrigal (INB0001496381). Playa San Miguel (9°34′39.3620N, 85°08′05.5470), Cabo Blanco, Provincia Puntarenas, 0 m depth, 13 November 1995, leg. F. Alvarado (INB0003096615). 1.5 km northwest of Playa Junquillal (10°58′40.7139N, 85°42′27.2867W), Bahía Junquillal, Provincia Guanacaste, 20 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003453953). 200 m northwest of Playa Guaria (10°57′55.1620N, 85°42′23.7922W), Bahía Junquillal, Provincia Guanacaste, 8 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003458479). Between Isla Bolaños and Playa Coyotera (11°02′51.0971N, 85°43′21.1040), Bahía Salinas, Provincia Guanacaste, 12 m depth, 10 April 2002, 3 shells, leg. F. González (INB0003502789). 1.5 km west of Puerto Soley (11°02′35.2251N, 85°41′47.9633W), Bahía Salinas, 10 m depth, 10 April 2002, 8 shells, leg. F. González (INB0003503459).1 km west of Playa Junquillal (10°58′24.5393N, 85°42′04.1590W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 5 April 2002, 17 shells, leg. F. González (INB0003503569). 400 m west of Isla Cabo Blanco (9°32′29.2960N, 85°07′16.0340W), Cabo Blanco, Provincia Puntarenas, 20–50 m depth, 16 May 1998, 14 shells, leg. A. Berrocal (INB0003539964). Between Punta Piedra and Punta Gallardo (8°35′47.5010N, 83°11′58.9990W), Provincia Puntarenas, 30–35 m depth, 13 June 1997, 12 shells, leg. M. Madrigal (INB0003542480). Isla David (10°56′06.0000N, 85°42′53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 11 shells, leg. S. Ávila (INB0003575679). Playa Ballena (9°06′34.2870N, 83°41′46.4390W), Provincia Puntarenas, 1 m depth, 16 April 1996, 1 shell, leg. Y. Camacho (INB0003722811). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 12 March 1996, 2 shells, leg. Y. Camacho (INB0003722813).

Shell morphology.— Length up to 9 mm; width up to 3.5 mm in the largest specimen examined. Shell solid, elongate, fusiform, with almost parallel sides (Fig. 2D–E). Body whorl very

large; spire long and conical in some specimens (Fig. 2E) or short and compressed in others (Fig. 2D), with 2–3 whorls. Suture canaliculated. Protoconch flattened, about 1.5 whorls, 300 μm in diameter (Fig. 2F), attached to the teleoconch by the aperture. Umbilicus absent. Aperture very long, about 7/10 of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique, with a long, thin callus running from its anterior end to about 1/3–1/5 of the aperture length. Sculpture with fine spiral lines, crossed by faint axial lines, not visible in all specimens. Color uniformly whitish.

Anatomy.— Digestive system containing three smooth and irregular gizzard plates, all of them similar in shape and size (Fig. 2G). Radular formula 16 × 1.0.1 in a specimen from Bahía Potrero Grande (LACM 72-29.12). Lateral teeth hook-shaped with a number of small denticles on the single, curved cusp (Fig. 2H).

Geographic range.— Recorded from Baja California to Panama (Keen 1971).

Remarks.— Marcus (1977) considered that *Acteon wetherillii* Lea, 1833, the fossil type species of *Acteocina*, is either a member of the Retusidae or Cylichnidae, but different from the common usage of the name *Acteocina* by modern authors. Marcus (1977) was unable to determine the position of this species, so she decided to use the next available name for this genus, which is *Tornatina* A. Adams, 1850. Marcus (1977) also maintained *Utriculastra* as different from *Acteocina* because of anatomical differences in the number of denticles on the radular teeth and the position of the esophagus.

On the contrary, Mikkelsen and Mikkelsen (1984) commented that *Acteon wetherillii* is a synonym of the recent species *Acteocina canaliculata* (Say, 1826), and therefore the name *Acteocina* should be maintained as valid. A comparison of the original descriptions of *A. wetherillii* (Lea 1833) and the redescription of *A. canaliculata* by Mikkelsen and Mikkelsen (1984) revealed that their shell morphology is in fact very similar. Mikkelsen and Mikkelsen (1984) also added *Utriculastra* Thiele, 1925 and *Cylichnella* Gabb, 1873 to the synonymy of *Acteocina*, following Gosliner (1979) who regarded *Utriculastra* and *Cylichnella* as synonyms. *Utriculastra* was originally based on *A. canaliculata* (the type species by original designation), and, therefore, it is an objective synonym of *Acteocina*. However, *Cylichnella* differs considerably from *Acteocina* in shell morphology. Gosliner (1979) commented that *Cylichnella* has an involute spire whereas *Utriculastra* possesses a projecting apex. Despite these differences, he regarded these two genera as synonyms because of a similar anatomy.

Due to the remarkable differences in shell morphology between *Cylichnella* and *Acteocina*, these two genera are here maintained as distinct. Marcus (1977) and Mikkelsen and Mikkelsen (1984) revised several species of *Acteocina* and provided detailed anatomical descriptions. The diagnosis above is based on these two papers.

Adams (1852) described *Bulla infrequens* based on two shells collected from Panama. The shells were not illustrated and described as being cylindrical, with a long aperture having a thick columellar plait, a moderately elevated, deeply channeled spire, and a white and smooth surface.

Dall (1919) described *Acteocina magdalenensis* from Bahía Magdalena, Baja California Sur, Mexico, with similar characteristics to those of *Acteocina infrequens*. Examination of the holotype (USNM 218410) reveals no substantial differences with the lectotype of *A. magdalenensis* and therefore these two names are regarded as synonyms.

A second synonym is *Acteocina angustior* described by Baker and Hanna (1927) from Puerto Escondido, Baja California, Mexico. The description and features of the holotype (CASIZ 032116) are undistinguishable from those of *Acteocina infrequens*. Baker and Hanna (1927) compared *A. angustior* with *Acteocina culcitella* Gould, 1852 (a northern species), but not with other Panamic species.

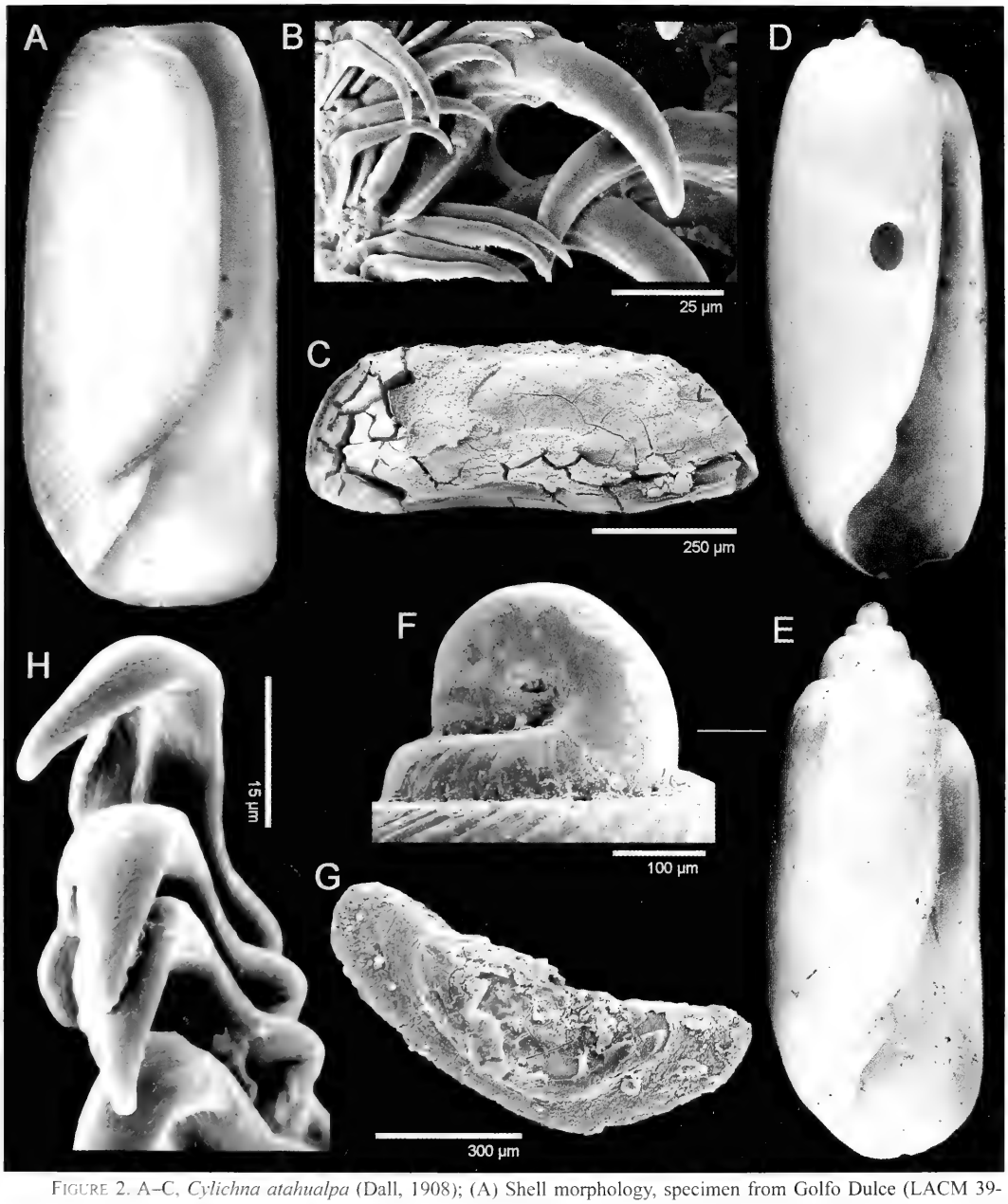

FIGURE 2. A–C, *Cylichna atahualpa* (Dall, 1908); (A) Shell morphology, specimen from Golfo Dulce (LACM 39-44.23), 6.5 mm long; (B) Radular teeth, specimen from Golfo Dulce (LACM 39-44.23); (C) Gizzard plate, same specimen. D–H, *Acteocina infrequens* (C.B. Adams, 1852); (D) Shell morphology, specimen from Isla Cabo Blanco (INB0003539964), 8 mm long; (E) Shell morphology, specimen from Bahía Cuajiniquil (INB0003575679), 4 mm long; (F) Protoconch, specimen from Playa Junquillal (INB0003503569); (G) Gizzard plate, specimen from Bahía Potrero Grande (LACM 72-29.12); (H) Radular teeth, same specimen.

***Acteocina carinata* (Carpenter, 1857)**
(Figs. 3A–C)

Tornatina carinata Carpenter, 1857:171.

Type material.— *Tornatina carinata*: Syntypes (6): Mazatlán, Mexico (BMNH).

Material examined.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 25 shells (CASIZ 170719). Puerto Culebra (10°35′N, 85°40′W), Provincia Guanacaste, 31 m depth, 13 March 1934, 1 shell (LACM 33-153.10). Puerto Culebra, (10°37′N, 85°40′W), Provincia Guanacaste, 27 m depth, 26 February 1934, 2 shells (LACM 34-253.5). Playa Blanca, Bahía Playa Blanca, Provincia Guanacaste (10°56′45″N, 85°53′30″W), 3–5 m depth, 8 February 1935, 3 shells (LACM 35-100.7). Puerto Parker (10°57′50″N, 85°48′45″W), Golfo Santa Elena, 55 m depth, 9 February 1935, 2 shells (LACM 35-113.24). Bahía Salinas (11°03′33″N, 85°43′47″W), 11 February 1935, 3 shells (LACM 35-117.15). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo, (10°57′20″N, 85°46′08″W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 15 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.44). Half mile to one mile and half west of Roca Vagares, Bahía de San Juanillo (10°57′28″N, 85°45′20″W), Provincia Guanacaste, 37 m depth, 14 February 1972, 1 shell, leg. D. Cadien and P. LaFollette (LACM 72-13.32). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02′22″N, 85°45′16″W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 4 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.43). Bahía Potrero Grande (10°50′56″N, 85°48′35″W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 7 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.10). Five miles north west of Islas Huevos (10°41′45″N, 85°46′25″W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-34.27). Middle of Bahía Huevos, north of Bahía Culebra (10°38′41″N, 85°41′55″W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 6 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.40). Half mile off mouth of Bahía Huevos (10°38′22″N, 85°42′52″W), Provincia Guanacaste, 36–42 m depth, 19 February 1972, 7 shells, leg. P. LaFollette and D. Cadien (LACM 72-36.24). Off beach at Bahía Brasilito (10°25′57″N, 85°49′18″W), Provincia Guanacaste, 18 m depth, 20 February 1972, 18 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.30). Anchorage at Bahía Ballena off Tambor (10°44′10″N, 84°59′34″W), Provincia Puntarenas, 10 m depth, 21 February, 1972, 1 shell, leg. P. LaFollette and A. Ferreira (LACM 72-43.17). Off beach at Bahía Ballena (9°44′12″N, 84°59′32″W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 5 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.38). Islet and rocks 1 km west of Isla Alcatraz (9°47′N, 84°53.5′W), Islas Tortugas, Provincia Puntarenas, 2–8 m depth, 23–24 February 1972, 1 shell, leg. P. LaFollete, D. Cadien, and A. Ferreira (LACM 72-46.58). Bahía Herradura (9°37′58″N, 84°40′30″W), Provincia Puntarenas, 21 m depth, 9 March 1972, 13 shells, leg. J. McLean (LACM 72-53.29). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 27 shells, leg. J. McLean (LACM 72-54.51). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22′43″N, 84°09′41″W), Provincia Puntarenas, 21 m depth, 11 March 1972, 1 shell, leg. J. McLean (LACM 72-57.38). Small islets of Quepos (9°22′12″N, 84°09′15″W), Provincia Puntarenas, 23 m depth, 12 March 1972, 5 shells, leg. J. McLean (LACM 72-59.30). South of Punta Uvita to Isla Ballena (9°07′36″N, 83°44′30″W), Provincia Puntarenas, 18 m depth, 13 March 1972, 1 fragment, leg. J. McLean (LACM 72-61.23). Off Isla del Caño (8°45′N, 83°54′W), Provincia Puntarenas, 55 m depth, 16–17 March 1972, 1 shell, leg. J. McLean (LACM 72-66.39). From Punta Piedra to Punta Gallardo (8°35′47.5010N, 83°11′58.9990W), Golfo Dulce, Provincia Puntarenas, 35 m depth, 13 June 1997, 1 shell, leg. M. Madrigal (INB0001496191). Playa San Miguel (9°34′39.3620N, 85°08′05.5470W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 0 m depth, 13 November 1995, 7 shells, leg. F. Alvarado (INB0003096504). 1.5 km northwest of Playa Junquillal (10°58′40.7139N, 85°42′27.2867W), Santa Rosa, Provincia Guanacaste, 20 m depth, 4 April 2002, 6 shells, leg. F. González (INB0003501408). Playa Naranjo (10°48′16.0960N, 85°41′12.0680W), Estero Real, Provincia Guanacaste, 0 m depth, 6 March 1995, 1 shell, leg. S. Ávila (INB0003539800). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 12 March 1996, 5 shells, leg. Y. Camacho (INB0003542874). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 12 March 1996, 5 shells, leg. Y. Camacho (INB0003542915). Isla David (10°56′32.2000N, 85°42′51.1000), Santa Rosa, Provincia

Guanacaste, 18 m depth, 4 shells, 12 March 1996, leg. Y. Camacho (INB0003575624). Isla David (10°56′06.0000N, 85°42′53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 21 shells, leg. Y. Camacho (INB0003575670). 1 km east of Punta Cirial (9°56′10.2222N, 84°52′43.1248W), Isla San Lucas, Provincia Puntarenas, 22.6 m depth, 9 December 1999, 1 shell, leg. M. Calderón (INB0003722804). 400 m west of Isla Cabo Blanco (9°32′29.2960N, 85°07′16.0340W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 20–50 m depth, 16 May 1998, 6 shells, leg. A. Berrocal (INB0003722806). Golfo de Papagayo (10°22′00.0000N, 86°15′00.0000W), 100 m depth, 10 February 1995, 2 shells, leg. Y. Camacho (INB0003722814). Dock of Playa San Miguel (9°34′36.9190N, 85°08′06.3610W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 0 m depth, 2 May 1995, 4 shells, leg. G. Mena (INB0003722818). Punta Oliva (9°34′39.3370N, 85°08′15.3840W), Cabo Blanco, Provincia Puntarenas, 0 m depth, 16 September 1995, 4 shells, leg. F. Alvarado (INB0003722821). La Viuda Rock (8°36′56.0065N, 83°14′08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 1 shell, leg. M. Lobo (INB0003722824). Golfo Santa Elena (10°58′45.4310N, 85°43′01.8500W), Bahía Junquillal, Provincia Guanacaste, 0–3 m depth, 13 March, 1996, 31 shells, leg. R. Angulo (INB0003722830). Boca de Estero Bocón (8°32′57.0600N, 83°18′51.2380W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 13 June 1995, 1 shell, leg. M. Lobo (INB0003747047). La Viuda Rock (8°36′56.0065N, 83°14′08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 23 shells, leg. M. Lobo (INB0003747054).

Shell morphology.— Length up to 4 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with almost parallel sides (Fig. 3A–B). Body whorl very large; spire short, with 3 whorls, flattened in some specimens (Fig. 3A) and conical in others (Fig. 3B). Suture not channeled. Posterior end of the whorls with an ornated sharp ridge (carina) with longitudinal bands. Protoconch flattened, about 1.2 whorls, 200 μm in diameter (Fig. 3C). It is only attached to the teleoconch by the aperture. Umbilicus absent. Aperture very long, between $^{7}/_{10}$ and $^{9}/_{10}$ of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique, with a thin callus running from its anterior end to about $^{1}/_{5}$–$^{1}/_{7}$ of the aperture length. Sculpture with fine spiral lines, crossed by faint axial lines, not visible in all specimens. Color uniformly whitish.

Anatomy.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

Geographic range.— Known from the Gulf of California to Costa Rica (Keen 1971).

Remarks.— Carpenter (1857) described this species as different from *Acteocina infrequens* by having a more irregular spire, a suture not channeled and a shoulder sharply carinated. Additionally, the shell of *A. infrequens* is elongate, with the end of the whorls rounded and the protoconch is about 300 μm in diameter, whereas the shell of *Acteocina carinata* has the posterior end of the whorls with a sharp ridge ornated with longitudinal bands and the protoconch is about 200 μm in diameter.

Acteocina harpa (Dall, 1871), originally described from California by Dall (1871) has a shell morphology similar to that of *A. carinata*, but according to Gosliner (1996), the former differs by having more assymetrical gizzard plates and a rachidian tooth with fewer denticles.

Acteocina sp. 1

(Figs. 3D–E)

Material examined.— 0.9 mile off beach at Bahía Potrero (10°27′42″N, 85°48′15″W), Provincia Guanacaste, 16–18 m depth, 20 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-39.13). Off beach at Bahía Brasilito (10°25′57″N, 85°49′18″W), Provincia Guanacaste, 18 m depth, 20 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-40.31).

Shell morphology.— Length up to 4.5 mm; width up to 2.5 mm in the largest specimen examined. Shell fragile, oval, with a convex right side and concave left side (Fig. 3D). Body whorl

very large; spire short and conical, with 1–2 whorls. Suture canaliculated. Protoconch flattened, about 1.5 whorls, 150 μm in diameter (Fig. 3E). Umbilicus absent. Aperture very long, about 4/5 of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique, with a long, thick callus. Sculpture with fine spiral lines, crossed by faint axial lines, not visible in all specimens. Color uniformly whitish.

Anatomy.— All the specimens examined consisted of empty shells, so anatomical examinations were not possible.

Geographic range.— This species is only known from Costa Rica (present paper).

Remarks.— This appears to be a distinct species of *Acteocina*, but it is not described herein because of the absence of anatomical data.

Acteocina sp. 1 is easily distinguishable from both *Acteocina infrequens* and *Acteocina carinata* by its shell morphology. The shell of *Acteocina* sp. 1 is shorter, more oval than that of *A. infrequens* and most specimens of *A. carinata*. In addition, the spire of *Acteocina* sp. 1 is shorter than in the other two species and the posterior end of the whorl lacks the sharp ridge ornated with longitudinal bands of *A. carinata*. The protoconch of *Acteocina* sp. 1 is considerably smaller than in the other two species.

Acteocina sp. 2

(Figs. 3F–G)

Material examined.— Puerto Jiménez (8°32.5′N, 83°19.5′W), Golfo Dulce, Provincia Puntarenas, 20 March, 1972, 1 shell, leg. J. McLean (LACM 72-69.17). Bahía El Hachal (10°56′08.9540N, 85°43′58.7890W), Provincia Guanacaste, 0 m depth, 15 September 1994, 2 shells, leg. C. Cano (INB0001480928). Boca de Estero Caballero (8°40′06.3050N, 83°26′41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 11 shells, leg. M. Lobo (INB0001499798). Quebrada Palma (8°39′06.8780N, 83°26′10.8200W), Playa Blanca, Golfo Dulce, Provincia Puntarenas, 0 m depth, 7 April 1995, >50 shells, leg. G. Mena (INB0003537637). Boca de Estero Caballero (8°40′06.3050N, 83°26′41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 11 shells, leg. M. Lobo (INB0003540727). Punta Palma (8°38′59.5510N, 83°26′07.5540W), Golfo Dulce, Provincia Puntarenas, 2 m depth, 12 June 1995, 7 shells, leg. M. Lobo (INB0003722822). 1 km south of Puntarenitas (8°36′55.7150N, 83°10′07.7110W), Provincia Puntarenas, 0 m depth, 13 May 1997, 1 shell, leg. S. Ávila (INB0003726899). Punta Palma (8°38′59.5510N, 83°26′07.5540W), Golfo Dulce, Provincia Puntarenas, 2 m depth, 12 June 1995, 31 shells, leg. M. Lobo (INB0003747326). Boca de Estero Bocón (8°32′57.0600N, 83°18′51.2380W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 13 June 1995, 7 shells, leg. M. Lobo (INB0003747047). Sector Playitas (8°44′19.1980N, 83°21′57.0660W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 10 February 1996, 2 shells, leg. M. Lobo (INB0003747549).

Shell morphology.— Length up to 3 mm; width up to 1.5 mm in the largest specimen examined. Shell fragile, elongate, posteriorly truncate, with almost parallel sides (Fig. 3F). Body whorl very large; spire short, almost flat. Suture canaliculated. Protoconch flattened, partially embedded in the teleoconch, 200 μm in diameter (Fig. 3G). Umbilicus absent. Aperture very long, about 9/10 of the shell length, narrow, wider anteriorly, narrowing gradually towards the posterior end. Columellar margin thickened, oblique. Sculpture with conspicuous spiral lines, more densely arranged near the anterior end of the shell, crossed by faint axial lines. Color uniformly whitish to pale brown.

Anatomy.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

Geographic range.— This species is only known from several localities in Costa Rica (present paper).

Remarks.— This appears to be a distinct species of *Acteocina*, but it is not described herein because of the absence of anatomical data.

This species is superficially similar to *Acteocina carinata* in shell morphology, but these two species are easily distinguishable by the presence of a shorter spire in *Acteocina* sp. 2, with the protoconch partially embedded in the teleoconch. Additionally, the sculpture of *Acteocina* sp. 2 has conspicuous spiral lines, more densely arranged near the anterior end of the shell, which are absent in *A. carinata*.

Genus *Cylichnella* Gabb, 1873

Cylichnella tabogaensis (Strong and Hertlein, 1939)

(Figs. 4A–C)

Retusa tabogaensis Strong and Hertlein, 1939:191–192, pl. 18, fig. 4.

Type material.— *Retusa tabogaensis*: Paratype: off Isla Taboga, Panama (LACM 1341).

Material examined.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 9 shells (CASIZ 170717). Bahía Cocos (10°33′35″N, 85°42′30″W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 2 shells (LACM 33-123.27). Puerto Culebra (10°35′N, 85°40′W), Provincia Guanacaste, 31 m depth, 13 March 1934, 4 shells (LACM 33-153.11). Playa Blanca (10°56′45″N, 85°56′W), Provincia Guanacaste, 73 m depth, 8 February 1935, 1 shell (LACM 33-103.14). Bahía Salinas (11°03′33″N, 85°43′47″W), 11 February 1935, 2 shells (LACM 35-117.16). Southeast end of Bahía Santa Elena, approximately 0.5 mile offshore (10°55′15″N, 85°48′30″W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, 10 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.15). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57′20″N, 85°46′08″W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.46). Half mile to one mile and half west of Roca Vagares, Bahía San Juanillo (10°57′28″N, 85°45′20″W), Provincia Guanacaste, 37 m depth, 14 February 1972, 6 shells, leg. D. Cadien and P. LaFollette (LACM 72-13.34). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02′22″N, 85°45′16″W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.44). Five miles north west of Islas Huevos (10°41′45″N, 85°46′25″W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-34). 250 m off Punta Piedra (8°35′24.6720N, 83°11′26.3250), Provincia Puntarenas, 23 m depth, 14 April 1997, 8 shells, leg. M. Lobo (INB0001496380). Between Isla Bolaños and Playa Coyotera (11°02′51.0972N, 85°43′21.1040W), Provincia Guanacaste, 12 m depth, 10 April 2002, 1 shell, leg. A. Berrocal (INB0003539773). From 500 m off the beach to 2.5 km southeast (8°34′39.1040N, 83°11′29.6540W), Punta Piedra, Provincia Puntarenas, 14–90 m depth, 10 April 1997, 24 shells, leg. M. Madrigal (INB0003540314). Between Punta Piedra and Punta Gallardo (8°35′47.5010N, 83°11′58.9990W), Golfo Dulce, Provincia Puntarenas, 30–35 m depth, 13 June 1997, 11 shells, leg. M. Madrigal (INB0003540361). 1 Km northwest of Playa Coronado (9°59′54.1430N, 84°58′49.6030W), Isla Caballo, Provincia Puntarenas, 10 m depth, 7 December 1999, 2 shells, M. Calderón (INB0003542209). Isla David (10°56′32.2000N, 85°42′51.1000W), Provincia Guanacaste, 18 m depth, 12 March 1996, 7 shells, leg. Y. Camacho (INB0003575621). Isla David (10°56′06.0000N, 85°42′53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 3 shells, leg. Y. Camacho (INB0003575666). La Viuda Rock (8°36′56.0065N, 83°14′08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 1 shell, leg. M. Lobo (INB0003722823). Bahía Junquillal (10°59′13.0310N, 85°43′16.7950W), Golfo Santa Elena, Provincia Guanacaste, 3 m depth, 2 shells, 13 March 1996, leg. R. Angulo (INB0003722827). Golfo Santa Elena (10°58′45.4310N, 85°43′01.8500W), Bahía Junquillal, Provincia Guanacaste, 0–3 m depth, 13 March, 1996, 2 shells, leg. R. Angulo (INB0003722831). 250 m off Punta Piedra (8°35′24.6720N, 83°11′26.3250), Provincia Puntarenas, 23 m depth, 14 April 1997, 14 shells, leg. M. Lobo (INB0003747050). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 11 shells, leg. Y. Camacho (INB0003747059). Playa Mostrencal (10°59′47.3060N, 85°42′53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 3 shells, 13 March

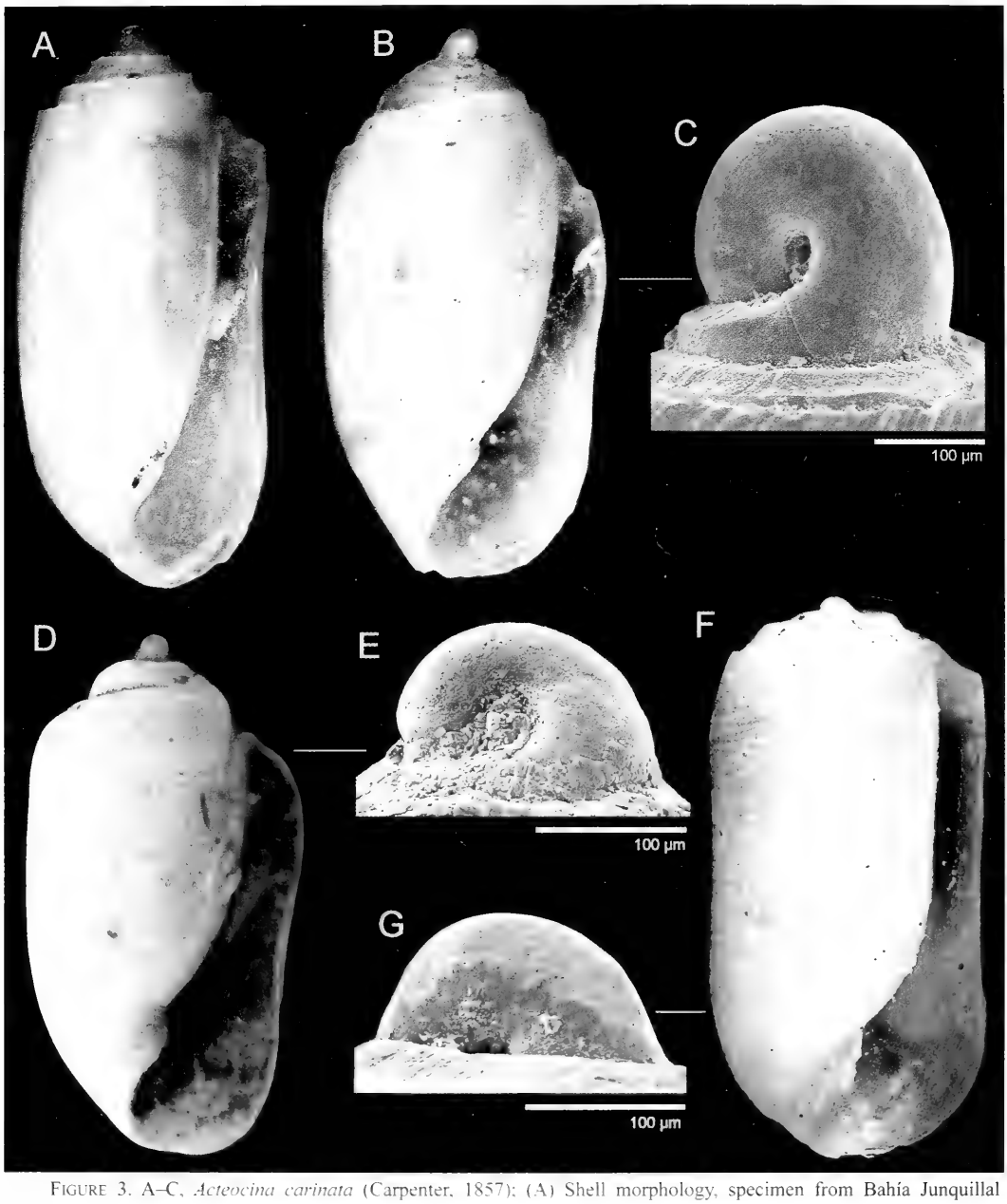

FIGURE 3. A–C, *Acteocina carinata* (Carpenter, 1857); (A) Shell morphology, specimen from Bahía Junquillal (INB0003722830), 4 mm long; (B) Shell morphology, specimen from Isla Cabo Blanco (INB0003722806), 4 mm long (C) Protoconch, specimen from Isla Cabo Blanco (INB0003722806). D–E, *Acteocina* sp. 1; (D) Shell morphology, specimen from Bahía Potrero (LACM 72-40.31), 4 mm long; (E) Protoconch, same specimen. F–G, *Acteocina* sp. 2; (F) Shell morphology, specimen from Golfo Dulce (INB0003747549), 2.5 mm long; (E) Protoconch, specimen from Golfo Dulce (INB0003537637).

1996, leg. R. Angulo (INB0003747411). 1 km east of Punta Cirial (9°56′10.2222N, 84°52′43.1248W), Isla San Lucas, Provincia Puntarenas, 0–22 m depth, 9 December 1999, 1 shell, leg. M. Calderón (INB0003747485).

Shell morphology.— Length up to 4 mm; width up to 2 mm in the largest specimen examined. Shell fragile, oval, with convex sides (Fig. 4A). Only one whorl visible, forming nearly the entire shell, except for a portion of the top of the spire. Apex rounded, umbilicated, with the aperture lip rising from the right side. Anterior end of the shell rounded. Aperture as long as the shell, wider anteriorly and narrowing gradually at about ⅙ of its length. Columellar margin conspicuously thickened with a small gap that divides the columella into two distinct folds. Umbilicus absent. Sculpture with a number of irregular spiral lines more conspicuous near the anterior and posterior ends of the shell. Color pale brown.

Anatomy.— Digestive system containing three smooth and irregular gizzard plates, composed of a thickened central area and a thinner extension (Fig. 4B). Central plate wider than the two lateral plates. Radular formula 16 × 1.1.1 in a specimen from Punta Piedra (INB0003540314). Lateral teeth hook-shaped with a wider area below the elongate cusp, bearing 16 long and strong denticles (Fig. 4C). Rachidian teeth broad, with several short denticles decreasing in size towards the laterals of each plate, and a gap with no denticles on the center of each rachidian tooth.

Geographic range.— This species is known from Panama and Costa Rica (Keen 1971).

Remarks.— *Retusa tabogaensis* was originally described based on several shells collected from Isla Taboga, Panama (Strong and Hertlein 1939). The most distinctive feature of this species was the presence of two denticles on the columella. Examination of the type material and original description revealed that our material from Costa Rica belongs to the same species.

Further anatomical examination of Costa Rican specimens revealed the presence of a radula with lateral teeth bearing an extension under the cusp with several long and strong denticles, and three gizzard plates, composed of a thickened central area and a thinner extension, one of the plates wider than the rest. All these features are consistent with those of *Cylichnella* Gabb, 1873, as defined by Gosliner (1979).

Cylichnella goslineri Valdés and Camacho-García, sp. nov.

(Figs. 4D–F, 5)

Type material.— *Cylichnella goslineri* sp. nov.: Holotype: Golfo Dulce, Provincia Puntarenas, 0 m depth, 10 February 1996, 1 specimen, leg. M. Lobo (INB0001497964).

Material examined.— Sector Playitas (8°44′19.1980N, 83°21′57.0660W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 10 February 1996, 15 specimens, leg. M. Lobo (INB0003718957). Four hundred and fifty meters southwest of Playa Blanca (10°03′39.5590N, 84°57′23.0410W), Provincia Puntarenas, 0 m depth, 8 December 1999, 1 shell, leg. M. Calderón (CASIZ 0121109).

Shell morphology.— Length up to 4.5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, oval to elongate, with convex sides (Fig. 4D). Only one whorl visible, forming nearly the entire shell, except for a visible portion of the top of the spire. Apex rounded, slightly umbilicated, with the aperture lip rising from the right side. Anterior end of the shell rounded. Aperture as long as the shell, wider anteriorly, narrowing gradually at about ⅕ of its length. Columellar margin slightly thickened, simple, with no folds or denticles. Umbilicus absent. Sculpture with a number of irregular and faint spiral lines. Color uniformly dirty white.

Anatomy.— Buccal bulb oval to elongate, connecting posteriorly to a short esophagus and the small salivary glands (Fig. 5A). Two strong retractor muscles attach laterally to the buccal bulb. Esophagus opening into a large gizzard, which contains three smooth and irregular gizzard plates, composed of a thickened central area and a thinner extension (Fig. 4E); central plate wider than the

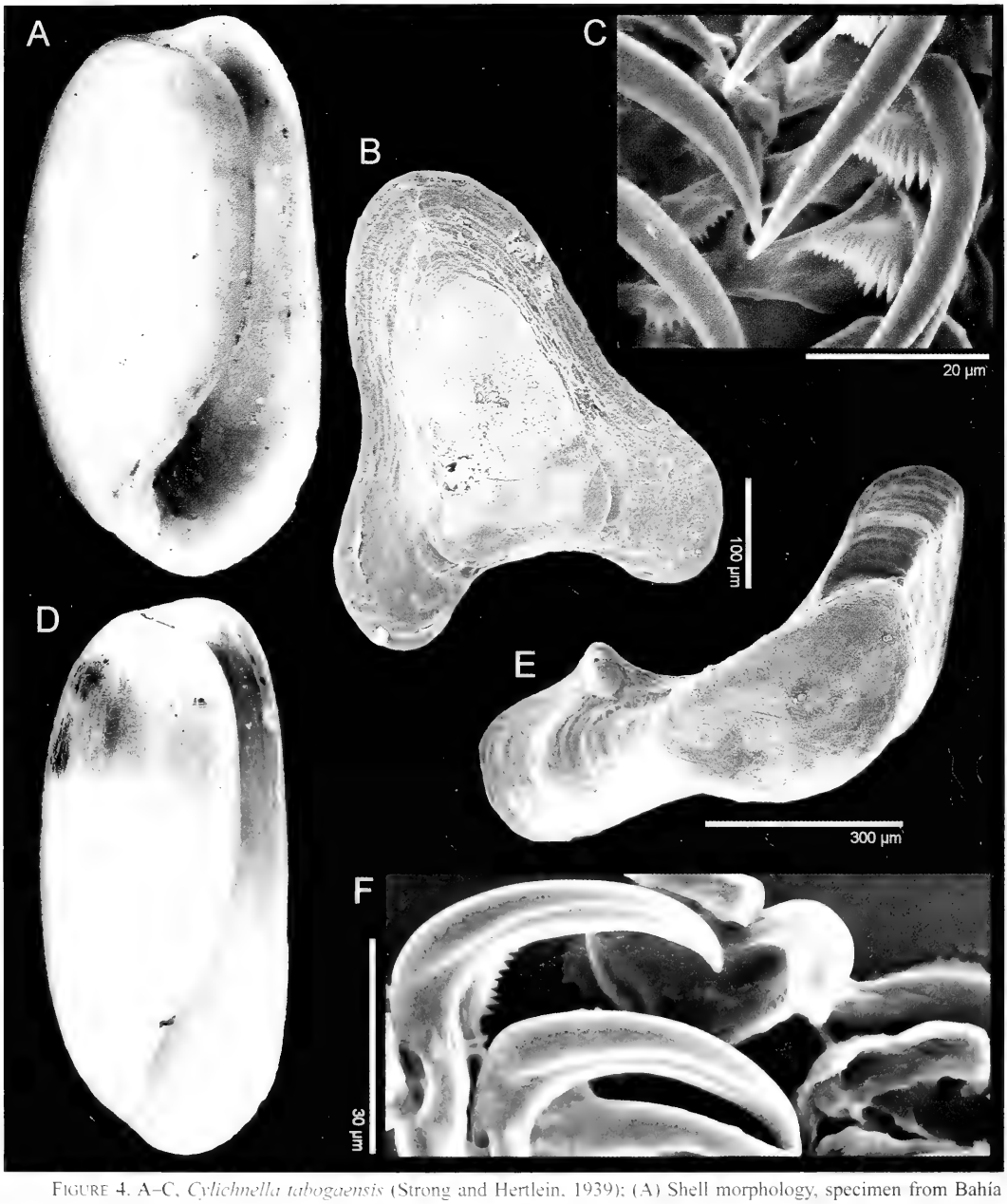

FIGURE 4. A–C, *Cylichnella tabogaensis* (Strong and Hertlein, 1939): (A) Shell morphology, specimen from Bahía Junquillal (INB0003747411), 4 mm long; (B) Central gizzard plate, specimen from Punta Piedra (INB0003540314); (C) Radular teeth, same specimen. D–F, *Cylichnella goslineri* sp. nov.: (D) Shell morphology, Holotype (INB0001497964), 4.5 mm long; (E) Lateral gizzard plate, Paratype from Golfo Dulce (INB0003718957); (F) Radular teeth, same specimen.

two lateral plates. Radular formula 21 × 1.1.1 in a specimen from Golfo Dulce (INB0003718957). Lateral teeth hook-shaped, with a wider area below the elongate cusp bearing 12 strong denticles (Fig. 4F). Rachidian teeth broad, with several short denticles decreasing in size towards the laterals of each plate, and a gap with no denticles on the center of each rachidian tooth.

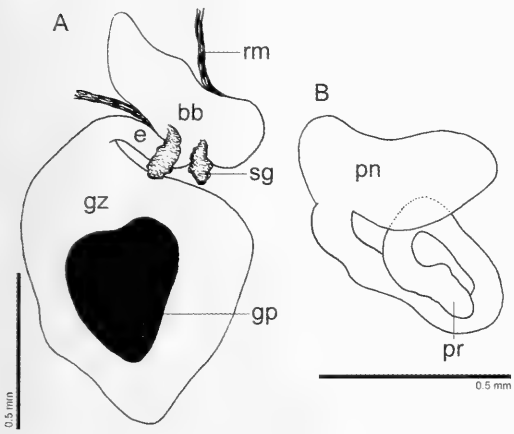

FIGURE 5. *Cylichnella goslineri* sp. nov., anatomy of specimen from Golfo Dulce (INB0003718957); (A) Anterior portion of the digestive system; (B) Male reproductive system. Abbreviations: bb, buccal bulb; e, esophagus; gp, gizzard plate; gz, gizzard; pn, penis; pr, prostate; rm, retractor muscule, sg, salivary gland.

Reproductive system monoaulic. Penis bulbous, connected to the prostate through a long and convoluted duct (Fig. 5B).

GEOGRAPHIC RANGE.— Known from Costa Rica (present paper).

ETYMOLOGY.— The species name is dedicated to our former advisor Terry Gosliner, for his company and support during the field work in Costa Rica.

REMARKS.— *Cylichnella goslineri* sp. nov. is clearly distinct from other *Cylichna*-like opisthobranchs described from the Panamic region by having a more elongate shell with no conspicuous spiral lines. The most similar species in shell morphology is *Cylichna atahualpa*, but these two species clearly differ in the morphology of the radula and gizzard plates (see above). The other member of the genus *Cylichnella* is *C. tabogaensis*, which has a shorter shell with conspicuous spiral lines and radular teeth with stronger denticles.

Cylichnella goslineri sp. nov. is assigned to the genus *Cylichnella* by having a radula with lateral teeth bearing an extension under the cusp with several long and strong denticles, and three gizzard plates, composed of a thickened central area and a thinner extension, one of the plates wider than the rest. All these features are consistent with the definition of this genus by Gosliner (1979).

Family Retusidae Thiele, 1925

Genus *Retusa* Brown, 1827

***Retusa paziana* Dall, 1919**
(Fig. 6A)

Retusa paziana Dall, 1919:297.

TYPE MATERIAL.— *Retusa paziana*: SYNTYPE: La Paz, Mexico (USNM 211418).

MATERIAL EXAMINED.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 22 m depth, 2 shells (CASIZ 170723). Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 16 shells (CASIZ 170724). Bahía Cocos (10°33′35″N, 85°42′30″W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 1 shell (LACM 33-123.28). Puerto Culebra (10°35′N, 85°40′W), Provincia Guanacaste, 31 m depth, 13 March 1934, 1 shell (LACM 33-153.12). Puerto Culebra (10°37′N, 85°40′W), 27 m depth, 26 February 1933, 1 shell (LACM 34-253.6). Puerto Parker (10°55′N, 85°49′W), Golfo Santa Elena, Provincia Guanacaste, 8 February 1935, 2 shells (LACM 35-138.2). Puerto Parker (10°57′50″N, 85°48′45″W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 3 shells (LACM 35-113.25). Bahía Salinas (11°03′33″N, 85°43′47″W), 11 February 1935, 3 shells (LACM 35.117.17). Bahía Salinas (11°03′33″N, 85°44′05″W), 11 February 1935, 2 shells (LACM 35-122.15). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57′20″N, 85°46′08″W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 3 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.47). Middle of Bahía Huevos, north of Bahía Culebra (10°38′41″N, 85°41′55″W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.41). Half mile off mouth of Bahía Huevos (10°38′22″N,

85°42′52″W), Provincia Guanacaste, 36–42 m depth, 19 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-36.25). Off beach at Bahía Brasilito (10°25′57″N, 85°49′18″W), Provincia Guanacaste, 18 m depth, 20 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-40.32). Off beach at Bahía Ballena (9°44′12″N, 84°59′32″W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.39). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 2 shells, leg. J. McLean (LACM 72-54.53). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 1 shell, leg. Y. Camacho (INB0003747060). Isla David (10°56′32.2000N, 85°42′51.1000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 18 m depth, 12 March 1996, 4 shells, leg. Y. Camacho (INB0003700589). Isla David (10°58′45.4310N, 85°43′01.8500W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 0–3 m depth, 13 March 1996, 3 shells, leg. R. Angulo (INB0003747335). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 3 shells, leg. Y. Camacho (INB0003719254).

Shell morphology.— Length up to 3 mm; width up to 1 mm in the largest specimen examined. Shell fragile, elongate, wider anteriorly and narrower posteriorly, with nearly parallel or slightly concave sides (Fig. 6A). Only one whorl visible, forming nearly the entire shell, except for a visible portion of the top of the spire and the apex of the protoconch, which is partially embedded. Apex umbilicated, with the aperture lip rising from the right side. Aperture lip forming a rounded wing connected to the columellar margin. Anterior end of the shell rounded. Aperture as long as the shell, wider anteriorly and narrowing abruptly at about ¼ of its length. Columellar margin slightly thickened. Columella simple, with no folds. Umbilicus absent. Sculpture with a number of conspicuous growth lines crossed by faint spiral lines. Color uniformly whitish.

Anatomy.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

Geographic range.— Known from the Gulf of California (Keen 1971) and Costa Rica.

Remarks.— Dall (1919) described *Retusa paziana* based on shells from La Paz, Baja California Sur, Mexico, with a short description and no figures. Baker and Hanna (1927) collected additional specimens from the Gulf of California and illustrated this species for the first time. The shells from Costa Rica here examined match the original description and redescription by Baker and Hanna (1927), and there is no doubt they belong to the same species.

Retusa paziana is the only member of *Retusa* from the Panamic region. Its unique shell morphology, with the wider area close to the anterior end, and the sculpture, composed of strong growth lines, make this species easily recognizable.

***Retusa* sp.**
(Fig. 6B)

Material examined.— 1.5 mile east of Punta Ballena (9°44′15″N, 84°33′45″W), Provincia Guanacaste, 3–15 m depth, 21–22 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-42.61). Playa Nancite (10°48′N, 85°42′W), north side of Golfo Papagayo, Provincia Guanacaste, 15 January 1986, 1 shell, leg. E. Coan and R. Hollywood (LACM 86-26.34).

Shell morphology.— Length up to 2 mm; width up to 1 mm in the largest specimen examined. Shell fragile, oval, wider near the center, with convex sides (Fig. 6B). Only one whorl visible, forming nearly the entire shell, except for a visible portion of the top of the spire and the apex of the protoconch, which is partially embedded. Apex umbilicated, with the aperture lip rising from the right side. Aperture lip forming a rounded wing connected to the columellar margin. Anterior end of the shell elongate. Aperture as long as the shell, wider anteriorly and narrowing gradually at about ¼ of its length. Columellar margin slightly thickened. Columella simple, with no folds.

Umbilicus very narrow. Sculpture with a number of simple spiral lines crossed by conspicuous growth lines. Color uniformly whitish.

Anatomy.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

Geographic range.— Known from Costa Rica (present paper).

Remarks.— This is most likely an undescribed species but it will not be described herein because of the lack of anatomical information. *Retusa* sp. is similar to *Retusa paziana* in some respects but clearly distinguishable by the outline of the shell and sculpture. The shell of *Retusa* sp. has its wider area near the center of the shell, whereas in *R. paziana* it is near the anterior end. Additionally, *Retusa* sp. has a small umbilicus that is absent in *R. paziana*. The sculpture of *R. paziana* is composed of conspicuous growth lines crossed by faint spiral lines whereas in *Retusa* sp. the spiral lines are equally conspicuous.

This species is provisionally placed in the genus *Retusa* because of the morphological similarities of the shell with some other species of the genus.

Genus *Volvulella* Newton, 1891

Volvulella cylindrica (Carpenter, 1864)

(Figs. 6D–E)

Volvula cylindrica Carpenter. 1864:179.
Volvulella callicera Dall. 1919:299.
Volvulella cooperi Dall. 1919:297–298.
Volvulella lowei Strong and Hertlein. 1937:164–165, pl. 35, fig. 2.

Type material.— *Volvula cylindrica*: Holotype: Santa Barbara, California (Redpath Museum 2364). *Volvulella callicera*: Holotype: Galapagos Islands (USNM 194976B). *Volvulella cooperi*: Holotype: Scammons Lagoon [= Laguna Ojo de Liebre], Baja California Sur, Mexico (USNM 105501). *Volvulella lowei*: Holotype: Puerto Escondido, Baja California Sur, Mexico (CASIZ 065971).

Material examined.— Puerto Parker, Golfo Santa Elena, Provincia Guanacaste, 27 m depth, 38 shells (CASIZ 170718). Bahía Cocos (10°33′35″N, 85°42′30″W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 2 shells (LACM 33-123.29). Puerto Culebra (10°35′N, 85°40′W), Provincia Guanacaste, 31 m depth, 13 March 1934, 4 shells (LACM 33-153.13). Puerto Culebra (10°37′N, 85°40′W), Provincia Guanacaste, 27 m depth, 26 February 1934, 1 shell (LACM 34-253.7). Puerto Parker (10°55′N, 85°49′W), Golfo Santa Elena, Provincia Guanacaste, 8 February 1935, 2 shells (LACM 35-138.3). Puerto Parker (10°57′50″N, 85°48′45″W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 2 shells (LACM 113.26). Bahía Salinas (11°03′33″N, 85°43′47″W), Provincia Guanacaste, 11 February 1935, 3 shells (LACM 35-117.18). Playa Blanca (10°56′45″N, 85°53′30″W), Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 7 shells (LACM 35-100.7). Playa Blanca (10°56′45″N, 85°53′30″W), Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 7 shells (LACM 35-100.7). Southeast end of Bahía Santa Elena, approximately half mile offshore (10°55′15″N, 85°48′30″W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, 8 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.16). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57′20″N, 85°46′08″W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-12.47). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02′22″N, 85°45′16″W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 3 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.45). Bahía Potrero Grande (10°50′56″N, 85°48′35″W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 6 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.11). Middle of Bahía Huevos, north of Bahía Culebra (10°38′41″N, 85°41′55″W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 18 shells,

leg. P. LaFollette and D. Cadien (LACM 72-35.42). Off beach at Bahía Brasilito (10°25′57″N, 85°49′18″W), Provincia Guanacaste, 18 m depth, 20 February 1972, 11 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.33). Anchorage at Bahía Ballena off Tambor (10°44′10″N, 84°59′34″W), Provincia Puntarenas, 10 m depth, 21 February, 1972, 2 shells, leg. P. LaFollette and A. Ferreira (LACM 72-43.18). Off beach at Bahía Ballena (9°44′12″N, 84°59′32″W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 5 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.40). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 11 shells, leg. J. McLean (LACM 72-54.54). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22′43″N, 84°09′41″W), Provincia Puntarenas, 21 m depth, 11 March 1972, 1 shell, leg. J. McLean (LACM 72-57.39). Playa Nancite (10°48′N, 85°42′W), north side of Golfo Papagayo, Provincia Guanacaste, 15 January 1986, 2 shells, leg. E. Coan and R. Hollywood (LACM 86-26.35). One km west of Playa Junquillal (10°58′24.5393N, 85°42′04.1590W). Bahía Junquillal, Provincia Guanacaste, 30 m depth, 1 shell, 5 April 2002, leg. F. González (INB0003503969). One and half km northwest of Playa Junquillal (10°58′40.7139N, 85°42′27.2867W), Bahía Junquillal, Provincia Guanacaste, 20 m depth, 1 shell, 4 April 2002, leg. F. González (INB0003539752). South of Isla Juanilla (10°58′55.1750N, 85°43′10.1707W), Murciélago, Provincia Guanacaste, 15 m depth, 1 shell, 9 April 2002, leg. F. González (INB0003539769). Between Isla Bolaños and Playa Coyotera (11°02′51.0972N, 85°43′21.1040), Bahía Salinas, Provincia Guanacaste, 12 m depth, 2 shells, 10 April 2002, leg. F. González (INB0003539771). Four hundred m west of Isla Cabo Blanco (9°32′29.2960N, 85°07′16.0340W), Cabo Blanco, Provincia Puntarenas, 20–50 m depth, 4 shells, 16 May 1998, leg. A. Berrocal (INB0003539975). Isla David (10°58′05.5000N, 85°42′38.6000), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 19 shells, 12 March 1996, leg. Y. Camacho (INB0003542912). Isla David (10°56′32.2000N, 85°42′51.1000), Santa Rosa, Provincia Guanacaste, 18 m depth, 16 shells, 12 March 1996, leg. Y. Camacho (INB0003575622). Playa Matapalo (9°21′48.1193N, 84°05′33.8006W), National Park Manuel Antonio, Provincia Puntarenas, 10–15 m depth, 1 shell, 18 February 2003, leg. F. González (INB0003708499). Playa Ballena (9°06′34.2870N, 83°41′46.4390W), Uvita, Provincia Puntarenas, 1 m depth, 1 shell, 16 March 1996, leg. Y. Camacho (INB0003722812). Muelle de la Playa San Miguel (9°34′36.9190N, 85°08′06.3610W), Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 0 m depth, 14 shells, 2 May 1995, leg. G. Mena (INB0003722819). Punta Oliva (9°34′39.3370N, 85°08′15.3840W), Cabo Blanco, Provincia Puntarenas, 0 m depth, 12 shells, 16 September 1995, leg. F. Alvarado (INB0003722820). Playa Mostrencal (10°59′47.3060N, 85°42′53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 2 shells, 13 March 1996, leg. R. Angulo (INB0003722825). Bahía Junquillal (10°59′13.0310N, 85°43′16.7950W), Golfo Santa Elena, Provincia Guanacaste, 3 m depth, 5 shells, 13 March 1996, leg. R. Angulo (INB0003722828). Isla David (10°58′45.4310N, 85°43′01.8500W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 0–3 m depth, 9 shells, 13 March 1996, leg. R. Angulo (INB0003747336). Isla David (10°56′06.0000N, 85°42′53.0000W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 18 m depth, 1 shell, 12 March 1996, leg. R. Angulo (INB0003747062).

Shell morphology.— Length up to 5.5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with nearly parallel sides (Fig. 6D–E). Only one whorl visible, forming the entire shell. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wider anteriorly, narrowing gradually at about ⅓ of its length. Aperture bended apically over the apex of the shell, with the parietal wall forming a conical spine that completely covers the apex. Spine long and more curved in some specimens (Fig. 6D) and shorter and straight in some others (Fig. 6E). Columellar margin thickened, with a small protuberance. Sculpture composed of a number of irregular spiral grooves crossed by numerous fine growth lines all over the shell surface. Spiral grooves situated near the anterior and posterior ends of the shell more conspicuous and separated from each other by wider gaps than those in the center of the shell. Color uniformly shiny whitish.

Anatomy.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

Geographic range.— Known from southern California to Panama and the Galapagos Islands (Keen 1971).

Remarks.— Carpenter (1864) described *Volvula cylindrica* from Santa Barbara, California,

based on a single shell. The original description is brief and offers few details. Examination of the holotype, illustrated by Palmer (1958), revealed that the specimens here examined match the original description of this species.

The shell morphology of this species is variable, with some specimens having a more elongate and curved apical spine and other specimens with a short and straight spine. The material examined includes intermediate forms within the entire range of variability.

This shell variability is probably the cause of the introduction of several names for this species. Three synonyms have been recognized in the Panamic Province: *Volvulella callicera* Dall, 1919, from the Galapagos, and *Volvulella cooperi* Dall, 1919 and *Volvulella lowei* Strong and Hertlein, 1937 from the Gulf of California. The study of the type material of all these species confirmed that they all fit within the variablility of *V. cylindrica*.

Volvulella californica Dall, 1919, originally described from southern California, was redescribed by Gosliner (1996), who argued that it is a distinct species from *V. cylindrica*. According to Gosliner (1996), *V. californica* is consistently devoid of sculpture and pyriform in shape, whereas *V. cylindrica* has a sculpture and is far more cylindrical.

Volvulella catharia Dall, 1919

(Fig. 6C)

Type material.— *Volvulella catharia*: Syntype: Bahía de Panama (USNM 211784).

Material examined.— Bahía Chatham (5°33′20″N, 86°59′10″W), Cocos Island, 26 m depth, 13 January 1938, 2 shells (LACM 38-179.5). Ten miles off Punta Guiones (9°43.5′N, 85°44.0′W), Provincia Guanacaste, 320–457 m depth, 13 May 1973, 2 shells (LACM 73-65.4).

Shell morphology.— Length up to 4 mm; width up to 2 mm in the largest specimen examined. Shell fragile, oval, with convex sides (Fig. 6C). Only one whorl visible, forming the entire shell. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wider anteriorly, narrowing gradually at about ¼ of its length. Aperture bended apically over the apex of the shell, with the parietal wall forming a short, blunt protuberance that covers the apex. Columellar margin thickened. Sculpture composed of irregular spiral grooves faded in the specimens examined. Color uniformly pale brown.

Anatomy.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

Geographic range.— Known from Costa Rica and Panama (Keen 1971).

Remarks.— Dall (1919) described *Volvulella catharia* as a small species with a short spine at the apex, subcylindrical and smooth. Examination of the holotype (USNM 211784) revealed that the specimens here studied from Costa Rica belong to the same species.

Volvulella catharia is clearly different from other Panamic species of *Volvulella*. The shell of *V. catharia* is shorter and proportionally wider, with a small and rounded apical extension. This species is provisionally placed in *Volvulella* until complete specimens become available for study.

Volvulella panamica Dall, 1919

(Fig. 6F)

Volvulella panamica Dall. 1919:298.
Volvulella tenuissima Willett. 1944:71–72, pl. 14, fig. 1.

Type material.— *Volvulella panamica*: Holotype: Bahía de Panama (USNM 212654). *Volvulella tenuissima*: Holotype: LACM 1073 (1 dry shell) 137 m, off Redondo Beach, Los Angeles County, California.

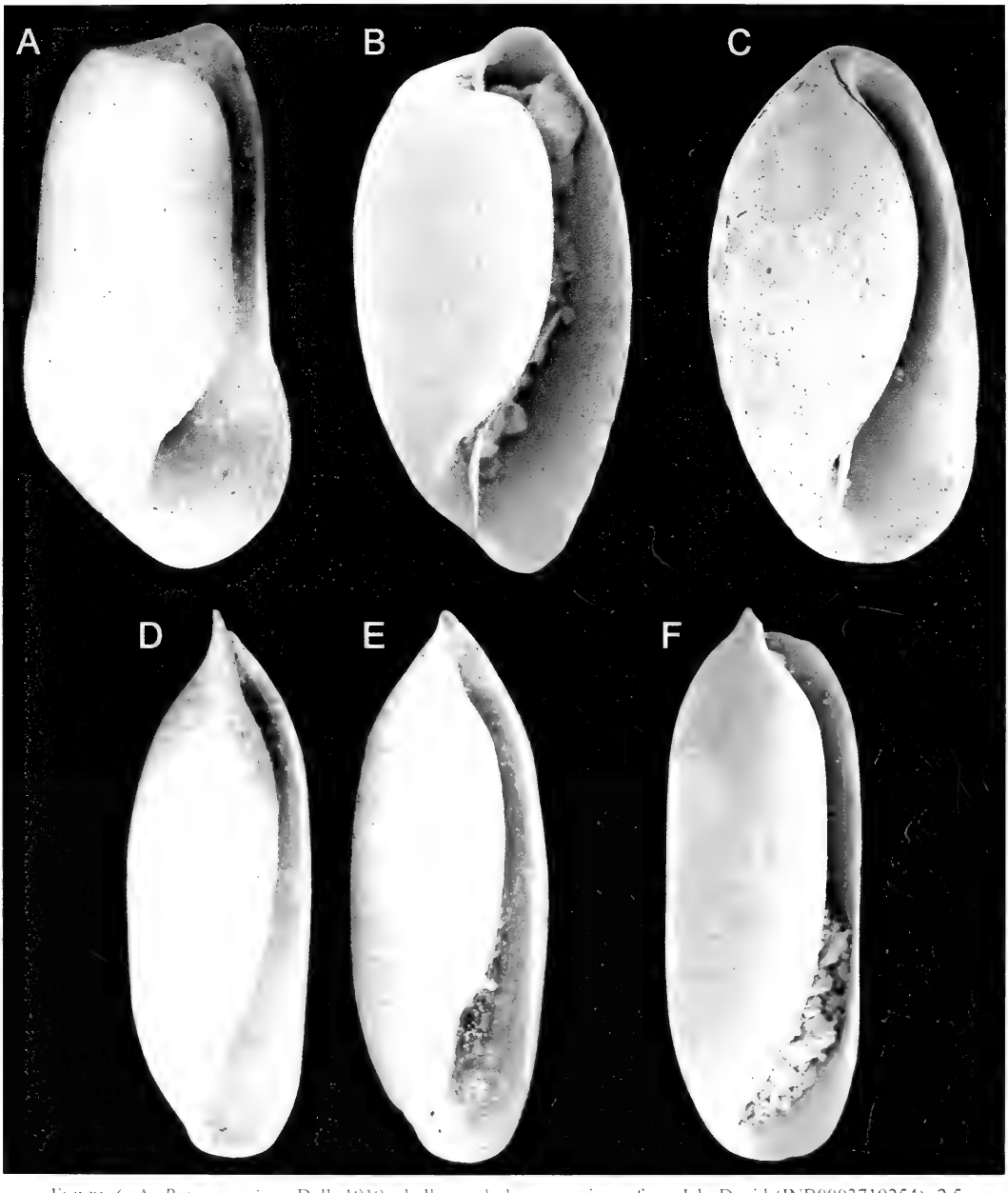

FIGURE 6. A, *Retusa paziana* Dall, 1919, shell morphology, specimen from Isla David (INB0003719254), 2.5 mm long. B, *Retusa* sp., shell morphology, specimen from Punta Ballena (LACM 72-42.61), 1.8 mm long. C, *Volvulella catharia* Dall, 1919, shell morphology, specimen from Punta Guiones (LACM 73-65.4), 4 mm long. D–E, *Volvulella cylindrica* (Carpenter, 1864): (D) Shell morphology, specimen from Bahía Junquillal, (INB0003747336), 5 mm long; (E) Shell morphology, specimen from Bahía Brasilito, 4 mm long (LACM 72-40.33). F, *Volvulella panamica* Dall, 1919, shell morphology, specimen from Bahía Herradura (LACM 72-54.55), 5.5 mm long.

Material examined.— Bahía Cocos (10°33′35″N, 85°42′30″W), south of Puerto Culebra, Provincia Guanacaste , 4 m depth, 13 March 1933, 2 shells (LACM 33-123.30). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 7 shells, leg. J. McLean (LACM 72-54.55).

Shell morphology.— Length up to 5.5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with nearly parallel sides (Fig. 6F). Only one whorl visible, forming the entire shell. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wider anteriorly, narrowing gradually at about ⅓ of its length. Aperture bended apically over the apex of the shell, with the parietal wall forming a short spine that completely covers the apex. Spine sharp and narrow because of the presence of a rounded notch on the posterior end of the spire. Columellar margin thickened, with a small protuberance. Sculpture composed of a number of irregular spiral grooves crossed by numerous fine growth lines all over the shell surface. Spiral grooves situated near the anterior and posterior ends of the shell more conspicuous and separated from each other by wider gaps than those in the center of the shell. Color uniformly shiny whitish.

Anatomy.— All the specimens examined consisted of empty shells so anatomical examinations were not possible.

Geographic range.— This species in known from southern California to Panama (Keen 1971; Gosliner 1996).

Remarks.— *Volvulella panamica* was described by Dall (1919) on the basis of a single shell from Panama Bay that had a very short and sharp apical spine. Examination of the holotype (USNM 212654) revealed that the spine morphology is caused by the presence of a rounded notch on the posterior end of the spire, not by shell damage or a preservation artifact. Examination of several shells from Costa Rica of different sizes revealed a similar morphology of the apex, which sustains the separation of this species from *Volvulella cylindrica.*

Volvulella tenuissima, originally described from southern California by Willett (1944) has a similar morphology and constitutes a synonym. The study of the holotype (LACM 1073), showed the presence of the sharp apical spine typical of this species.

Family Haminoeidae Pilsbry, 1895

Genus *Haminoea* Turton, 1830

Haminoea ovalis Pease, 1868

(Figs. 7A, 8A–C, 9)

Haminoea ovalis Pease, 1868:71, pl. 7, fig. 2, pl. 12, fig. 20.

Type material.— *Haminoea ovalis*: Untraceable.

Material examined.— Punta Uvita (9°08′44.4560N, 83°45′42.2750W), Provincia Puntarenas, 0 m depth, 1 shell, 13 April 1996, leg. R. Angulo (INB0001486877). 500 m south of Playa Ventanas (9°05′16.1660N, 83°40′50.7600W), Provincia Puntarenas, 0 m depth, 2 specimens, 17 January 2000, leg. M. Calderón (INB0001495966). 500 m south of Playa Ventanas (9°05′16.1660N, 83°40′50.7600W), Provincia Puntarenas, 0 m depth, 1 specimen, 17 January 2000, leg. M. Calderón (INB0001496120). San Miguel (9°34′49.0680N, 85°08′28.5260), Cabo Blanco, Provincia Puntarenas, 2 m depth, 16 May 1998, 1 specimen, leg. A. Berrocal (INB0001496693). San Miguel (9°34′49.0680N, 85°08′28.5260), Cabo Blanco, Provincia Puntarenas, 2 m depth, 16 May 1998, 1 specimen, leg. A. Berrocal (INB0001496694). Puerto Escondido (9°23′02.7920N, 84°08′14.4875W), National Park Manuel Antonio, Provincia Puntarenas, 0 m depth, 3 specimens, 19 February 2003, leg. A. Berrocal (INB0003572107). National Park Manuel Antonio (9°23′02.6451N, 84°10′05.9237W), Provincia Puntarenas, 8–11 m depth, 1 specimen, 19 February 2003, leg. A. Berrocal (INB0003572120). Isla Ballena (9°06′18.0003N, 83°43′42.7017W), Provincia Puntarenas, 18 m depth, 18 January 2003, 1 specimen, leg. S. Ávila (INB0003572558). Isla Santa Catalina (10°28′37.2000N,

85°52′06.6000W), Provincia Guanacaste, 15 m depth, 21 July 2000, 2 specimens, leg. M. Calderón (INB0003701269).

Shell morphology.— Length up to 4 mm; width up to 3 mm in the largest specimen examined. Shell fragile, delicate, oval, with convex sides (Fig. 8A). Only one whorl visible, forming the entire shell. Apex rounded, with the aperture lip rising from the left side. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wide anteriorly, narrowing gradually at about ½ of its length. Columellar margin slightly thickened. Surface smooth, the sculpture being reduced to fine growth lines. Color uniformly pale brown.

External morphology.— Body oval, 6 mm long in the largest specimen examined. Cephalic shield elongate, narrower posteriorly, comprising about ½ of the body length (Fig. 7A). Hancock's organs composed of about 6 simple folds each. Parapodia short and narrow, covering a small portion of the shell laterally. Posterior half of the body almost entirely covered by the shell. Gill unipinnate, with 15 simple lamellae. Color of living animals pale bluish gray, with darker areas on anterior central region of the cephalic shield and the posterior lateral sides, as well as in some irregular areas on the rest of the body. Entire surface of the body covered by small and bright orange dots. Shell translucent, almost transparent. Area covered by the shell clearly visible, with the same color as the rest of the body and the orange dots larger in diameter.

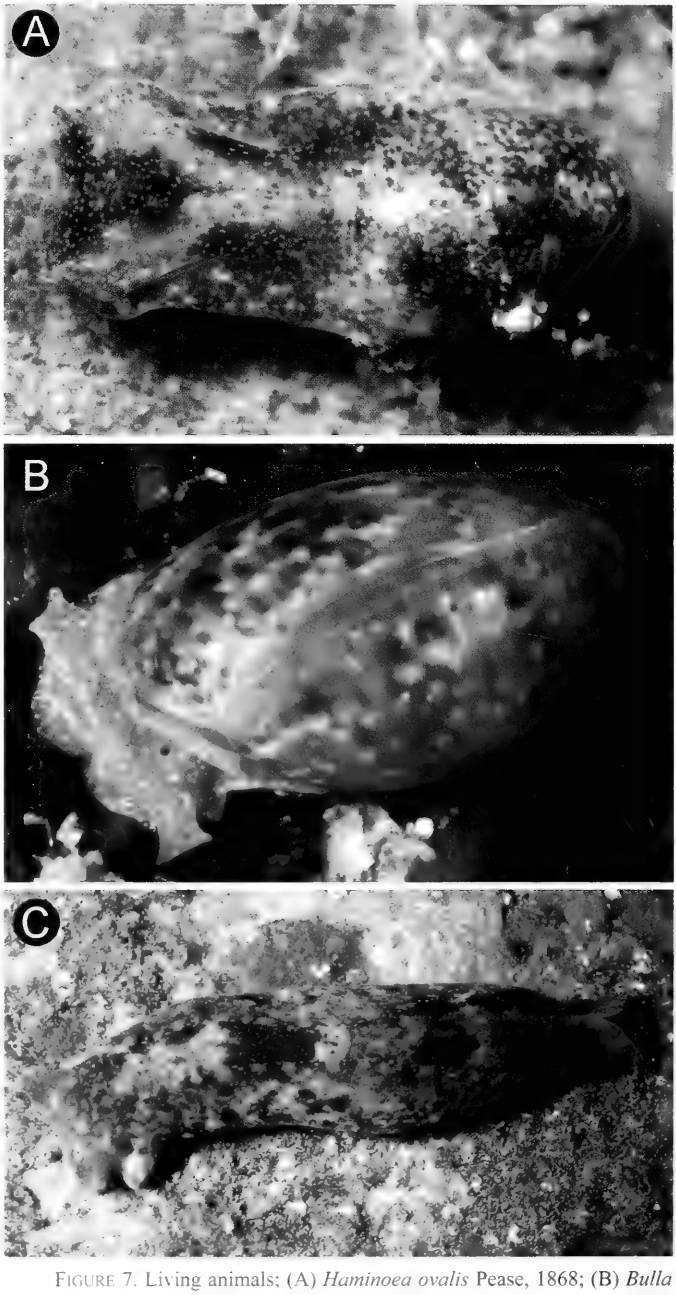

FIGURE 7. Living animals: (A) *Haminoea ovalis* Pease, 1868; (B) *Bulla punctulata* A. Adams in Sowerby, 1850; (C) *Navanax aenigmaticus* (Bergh, 1894).

Anatomy.— Buccal bulb oval to elongate, connecting posteriorly to a short esophagus and two long salivary glands (Fig. 9A). Esophagus opening into a large gizzard, which contains three

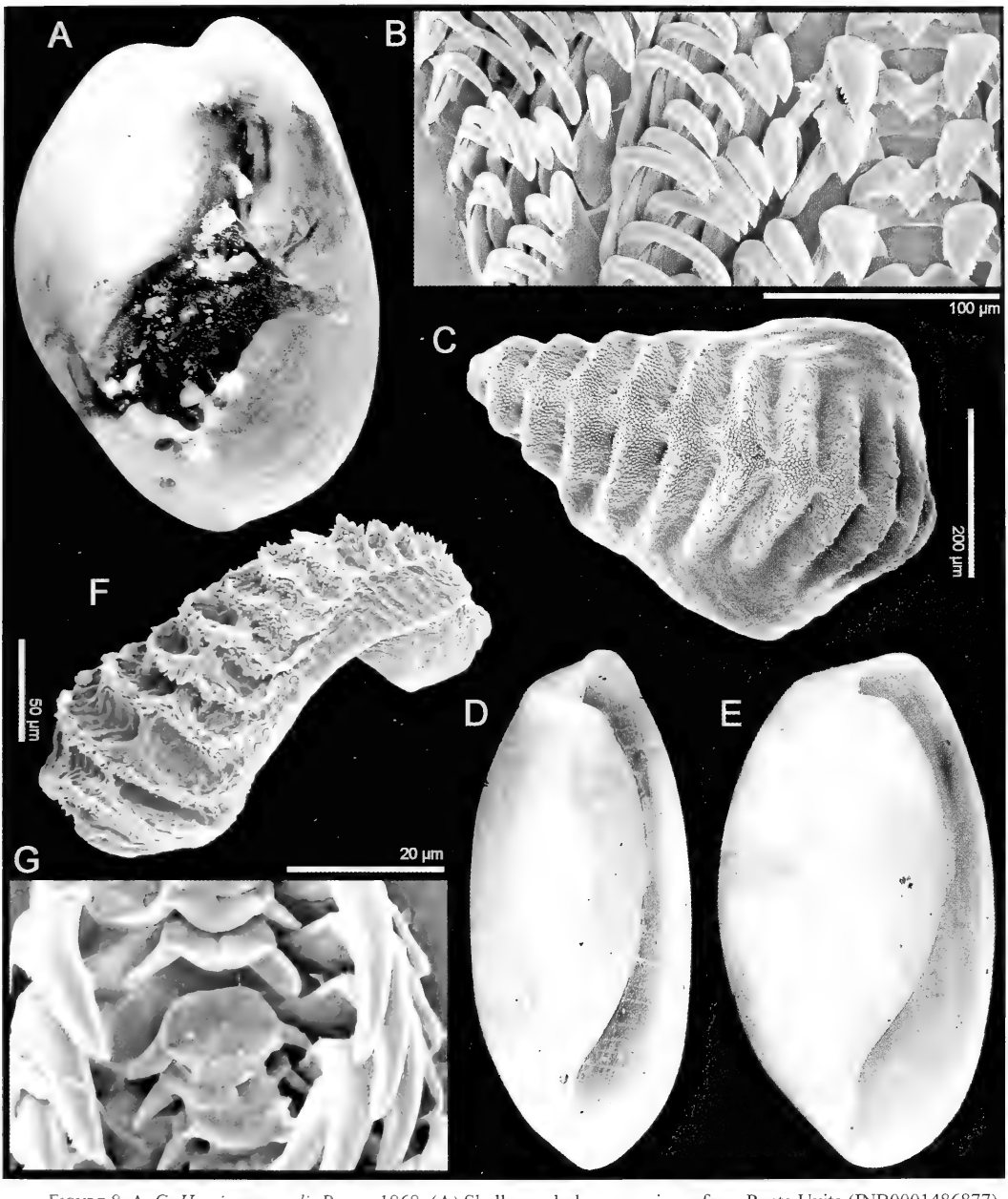

FIGURE 8. A–C, *Haminoea ovalis* Pease, 1868; (A) Shell morphology, specimen from Punta Uvita (INB0001486877), 4 mm long; (B) Radular teeth, specimen from Isla Ballena (INB0003572558); (C) Gizzard plate, same specimen. D–G, *Atys exarata* Carpenter, 1857; (D) Shell morphology, specimen from Punta Descartes (INB0003747331), 5 mm long; (E) Shell morphology, specimen from between Punta Piedra and Punta Gallardo (INB0003540313), 4 mm long; (F) Gizzard plate, specimen from Punta Piedra (INB0001496350); (G) Radular teeth, same specimen.

smooth and irregular gizzard plates. All plates are similar in shape and size, each one having a series of transverse, parallel ridges composed of several rows of small, simple denticles (Fig. 8C).

Radular formula 19 × 11.1.11 in a specimen from Isla Ballena (INB0003572558). First inner-

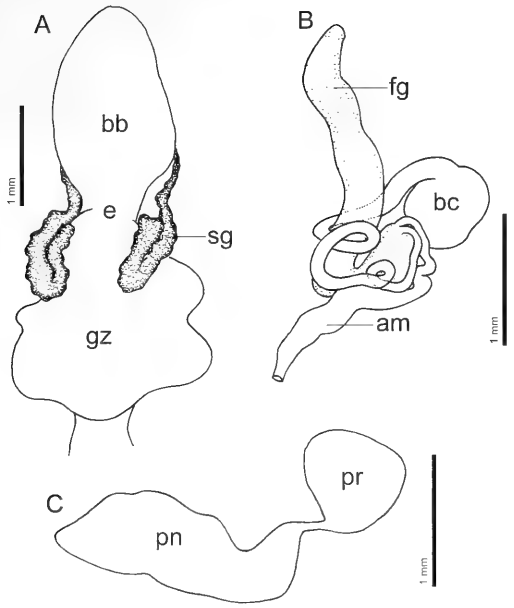

FIGURE 9. *Haminoea ovalis* Pease, 1868, anatomy of specimen from Isla Ballena (INB0003572558); (A) Anterior portion of the digestive system; (B) Female reproductive system; (C) Male reproductive system. Abbreviations: am, ampulla; bb, buccal bulb; bc, bursa copulatrix; e, esophagus; fg, female glands; gz, gizzard; pn, penis; pr, prostate; sg, salivary gland.

most teeth with a wide triangular cusp bearing several small denticles (Fig. 8B). Lateral teeth hook-shaped with a strong cusp lacking denticles. Rachidian teeth broad, with a wide base, a single central cusp, and one denticle on each side of the cusp.

Reproductive system monoaulic. Penis bulbous, connected to the prostate through a short duct (Fig. 9C). Ampulla long and convoluted, connecting to a short and wide postampullary duct that opens into the female glands. Bursa copulatrix entering the female glands (Fig. 9B).

GEOGRAPHIC RANGE.— This is a widespread Indo-Pacific species. This is the first record of the species for the eastern Pacific.

REMARKS.— The specimens here examined resemble the external coloration of *Haminoea ovalis* Pease, 1868, originally described from Tahiti, French Polynesia. *Haminoea angelensis* Baker and Hanna, 1927, was described on the basis of shell morphology (Baker and Hanna 1927), so it is impossible to determine its taxonomic status. Two other Panamic species, *Haminoea vesicula* (Gould, 1855) and *Haminoea virescens* (Sowerby, 1833) have been illustrated by Behrens (1991) and clearly differ from *H. ovalis* by lacking the bright orange spots characteristic of this species.

Genus *Atys* de Monfort, 1810

Atys exarata (Carpenter, 1857)

(Figs. 8D–G)

Bulla exarata Carpenter, 1857:173.
Atys casta Carpenter, 1864:314.
Atys chimera Baker and Hanna, 1927:126, pl. 4, fig. 4.
Cylichna veleronis Strong and Hertlein, 1939:191.
Cylichna stephensae Strong and Hertlein, 1939:190.
Atys liriope Hertlein and Strong, 1951:71, pl. 8, fig. 2.

TYPE MATERIAL.— *Bulla exarata*: HOLOTYPE: Mazatlán, Sinaloa, Mexico (BMNH). *Atys casta*: LECTOTYPE and PARALECTOTYPE: Cabo San Lucas, Baja California Sur, Mexico (USNM 4014). *Atys chimera*: HOLOTYPE: Puerto Escondido, Baja California Sur, Mexico (CASIZ 032115). *Cylichna veleronis*: PARATYPE: Bahía Honda, Isla Coiba, Panama (LACM 1340). *Cylichna stephensae*: PARATYPE: Bahía Honda, Isla Coiba, Panama (LACM 1339). *Atys liriope*: HOLOTYPE: Arena Bank, Gulf of California (CASIZ 065495).

MATERIAL EXAMINED.— Bahía Cocos (10°33′35″N, 85°42′30″W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 5 shells (LACM 33-123.31). Playa Blanca (10°56′45″N,

85°53′30″W), Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 7 shells (LACM 35-100.9). Playa Blanca (10°56′45″N, 85°53′30″W), Bahía Playa Blanca, Provincia Guanacaste, 73 m depth, 1935, 8 shells (LACM 35-103.15). Southeast end of Bahía Santa Elena, approximately half mile offshore (10°55′15″N, 85°48′30″W), Provincia Guanacaste, 9–12 m depth, 13 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-9.17). Southeast corner of Bahía Jobo, off sand beach west of Bahía Salinas (11°02′22″N, 85°45′16″W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 13 shells, leg. P. LaFollette and D. Cadien (LACM 72-19.46). Cove between Isla San José and Isla Cocinero (10°51′50″N, 86°55′30″W), Islas Murciélago, Provincia Guanacaste, 3–11 m depth, 17 February 1972, 1 shell, leg. P. LaFollette, D. Cadien and A. Ferreira (LACM 72-21.19). Middle of Bahía Huevos, north of Bahía Culebra (10°38′41″N, 85°41′55″W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 17 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.43). Off beach at Bahía Brasilito (10°25′57″N, 85°49′18″W), Provincia Guanacaste, 18 m depth, 20 February 1972, 16 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.34). Off beach at Bahía Ballena (9°44′12″N, 84°59′32″W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 7 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.41). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22′43″N, 84°09′41″W), Provincia Puntarenas, 21 m depth, 11 March 1972, 1 shell, leg. J. McLean (LACM 72-57.40). North side of Isla del Caño (8°43′15″N, 83°53′07″W), Provincia Puntarenas, 7–14 m depth, 14–19 March 1972, 6 shells, leg. J. McLean and D. Wheeler (LACM 72-63.80). 250 m off Punta Piedra (8°35′24.6720N, 83°11′26.3250W), Provincia Puntarenas, 23 m depth, 14 April 1997, 12 shells, leg. M. Lobo (INB0001496350). 1 km west of Playa Junquillal (10°58′24.5393N, 85°42′04.1590), Provincia Guanacaste, 30 m depth, 5 April 2002, 1 shell, leg. F. González (INB0003503527). 1 km west of Playa Junquillal (10°58′24.5393N, 85°42′04.1590), Provincia Guanacaste, 30 m depth, 5 April 2002, 1 shell, leg. F. González (INB0003503528). South of Isla Juanilla (10°58′55.1750N, 85°43′10.1707W), Murciélago, Provincia Guanacaste, 15 m depth, 2 shells, 9 April 2002, leg. F. González (INB0003504414). From 500 m off the beach to 2.5 km southeast (8°34′39.1040N, 83°11′29.6540W), Punta Piedra, Provincia Puntarenas, 14–90 m depth, 10 April 1997, 25 shells, leg. M. Madrigal (INB0003540313). Between Punta Piedra and Punta Gallardo (8°35′47.5010N, 83°11′58.9990W), Provincia Puntarenas, 30–35 m depth, 13 June 1997, 8 shells, leg. M. Madrigal (INB0003540366). 1 km west of Playa Junquillal (10°58′24.5393N, 85°42′04.1590W). Bahía Junquillal, Provincia Guanacaste, 30 m depth, 4 shells, 5 April 2002, leg. F. González (INB0003542436). Isla David (10°56′32.2000N, 85°42′51.1000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 2 shells, leg. Y. Camacho (INB0003575625). Isla David (10°56′06.0000N, 85°42′53.0000W), Bahía Cuajiniquil, Provincia Guanacaste, 18 m depth, 12 March 1996, 2 shells, leg. S. Ávila (INB0003575665). Playa Blanca (8°38′18.0525N, 83°26′15.7570W), Provincia Puntarenas, 0 m depth, 5 April 1995, 1 shell, leg. G. Mena (INB0003722817). Bahía Junquillal (10°58′45.4310N, 85°43′01.8500W), Provincia Guanacaste, 0–3 m depth, 1 shell, 13 March 1996, leg. R. Angulo (INB0003722829). Boca de Estero Caballero (8°40′06.3050N, 83°26′41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 1 shell, leg. M. Lobo (INB0003747046). Golfo Santa Elena (10°59′13.0310N, 85°43′16.7950W), Bahía Junquillal, Provincia Guanacaste, 3 m depth, 13 March, 1996, 1 shell, leg. R. Angulo (INB0003747330). Punta Descartes (11°02′21.8310N, 85°43′11.0470W), Playa Coyotera, Provincia Guanacaste, 0 m depth, 14 March 1995, 1 shell, leg. G. Bassey (INB0003747331).

Shell morphology.— Length up to 6 mm; width up to 3 mm in the largest specimen examined. Shell fragile, oval, with convex sides (Figs. 8D–E). Shell morphology very variable, some specimens are wider (Fig. 8E) whereas others are more elongate (Fig. 8D). Only one whorl visible, forming the entire shell. Apex rounded, depressed, not umbilicated, with the aperture lip conspicuously rising from the left side. The aperture lip forms a short wing posteriorly, longer in some specimens (Fig. 8D). Anterior end of the shell rounded. Umbilicus absent. Aperture long, wide anteriorly, narrowing at about ⅓ of its length continuing in a narrow canal to the end of the shell where it widens again. Columellar margin slightly oblique, with a thickened margin and no folds. Sculpture with a number of simple spiral grooves, less conspicuous in the middle area of the shell, and more densely concentrated near the anterior and posterior ends. Color uniformly whitish to pale gray.

Anatomy.— Digestive system with a gizzard containing three irregular gizzard plates. Each

plate has a series of transverse, parallel ridges composed of small, simple denticles (Fig. 8F). All plates are similar in shape and size. The radular formula is 23 × 5.1.5 in a specimen from Punta Piedra (INB0001496350). The innermost lateral teeth are hook-shaped with a long and strong cusp bearing numerous denticles (Fig. 8G). The remaining four lateral teeth have a simple cusp, with no denticles. The rachidian teeth are broad, with a triangular base and a wide central cusp lacking denticles.

Geographic range.— Known from southern California to Panama (Skoglund 2002).

Remarks.— *Bulla exarata* was introduced based on a shell collected from Mazatlán, Sinaloa, Mexico, with a short description with no illustrations. The holotype of this species (BMNH) is an elongate shell with numerous and conspicuous longitudinal striations and the aperture lip conspicuously rising from the left side. These and other features of the specimen are very similar to those of the material here examined.

A few years later, Carpenter (1864) described *Atys casta*, with a short text and no illustrations, based on a single shell collected from Cabo San Lucas, Baja California Sur, Mexico. Baker and Hanna (1927) considered the description of *A. casta* "so vague and indefinite that identifications based thereupon would be entirely untrustworthy." Consequently these authors introduced a new name, *Atys chimera* for similar shells collected from Puerto Escondido, La Paz, and Bahía Concepción, Baja California Sur, Mexico. A re-examination of a syntype of *Atys casta* (USNM 4014) revealed that this specimen is very similar in shell morphology to the specimens here examined, which also agrees with the original description of *A. chimera* and the features of the holotype (CASIZ 032115).

Three other synonyms of *Atys exarata* are *Cylichna veleronis* Strong and Hertlein, 1939, *Cylichna stephensae* Strong and Hertlein, 1939, and *Atys liriope* Hertlein and Strong, 1951. Both *C. veleronis* and *C. stephensae* were described based on shells dredged from Bahía Honda, Panama, and were only compared to species of *Cylichna*. Examination of the type material of these two taxa shows remarkable similarities with the material here examined and all the shells fit within the variability described for this species. *Cylichna stephensae* was described for wider shells with fewer and more distant spiral lines, whereas *C. veleronis* was described for narrower shells with more highly compressed spiral lines.

Atys liriope was described by Hertlein and Strong (1951) as different from *Atys chimera* by having a more closely spaced and conspicuous sculpture. These differences are explainable by the normal variability of the species, and there is no doubt that *A. lirope* is a synonym of *A. exarata*.

This species is placed in *Atys* because of the presence of transverse, parallel ridges composed of denticles in the gizzard plates, and the radular morphology, which has broad rachidian teeth, with a wide triangular base and a broad central cusp bearing numerous small denticles as well as hook-shaped lateral teeth with a long and strong cusp bearing numerous denticles on the inner lateral teeth.

Atys defuncta (Baker and Hanna, 1927)

(Figs. 10A–D)

Cylichnella defuncta Baker and Hanna, 1927:127–128, pl. 4, fig. 3.

Type material.— *Cylichnella defuncta*: Holotype: Bahía Amortajada, Isla San José, Baja California Sur, Mexico (CASIZ 032118).

Material examined.— Bahía Cocos (10°33′35″N, 85°42′30″W), south of Puerto Culebra, Provincia Guanacaste, 4 m depth, 13 March 1933, 2 shells (LACM 33-123.33). Puerto Culebra (10°35′N, 85°40′W), Provincia Guanacaste, 31 m depth, 13 March 1934, 8 shells (LACM 33-153.14). Bahía Chatham (5°33′N,

86°59′W), Cocos Island, 31 m depth, 28 February 1933, 7 shells (LACM 33-154.1). Puerto Parker (10°55′N, 85°49′W), Golfo Santa Elena, Provincia Guanacaste, 8 February 1935, 2 shells (LACM 35-138.4). Bahía Chatham (5°33′20″N, 86°59′10″W), Cocos Island, 26 m depth, 13 January 1938, 1 shell (LACM 38-179.6). Playa Blanca (10°56′45″N, 85°53′30″W), Bahía Playa Blanca, Provincia Guanacaste, 3–5 m depth, 8 February 1935, 29 shells (LACM 35.100.10). Puerto Parker (10°57′50″N, 85°48′45″W), Golfo Santa Elena, Provincia Guanacaste, 55 m depth, 9 February 1935, 9 shells (LACM 35-113.28). Bahía Salinas (11°03′33″N, 85°44′05″W), Provincia Guanacaste, 11 February 1935, 9 shells (LACM 35-122.17). Between Punta Isla and 500 m south of Punta Isla (10°56′00″N, 85°48′55″W), Bahía Santa Elena, Provincia Guanacaste, 1–11 m depth, 13 February 1972, 5 shells, leg. P. LaFollette and D. Cadien (LACM 72-7.34). One mile offshore, between Bahía Santa Elena and Bahía San Juanillo (10°57′20″N, 85°46′08″W), Provincia Guanacaste, 25–53 m depth, 14 February 1972, 2 shells, leg. P. LaFollette and D. Cadien (LACM 72-12.49). Southeast corner of Bahía Jobo, off sand beach west of Bahía de Salinas (11°02′22″N, 85°45′16″W), Provincia Guanacaste, 1–10 m depth, 14 February 1972, 24 shells, leg. P. LaFollette and D. Cadien (LACM 72-21.47). Cove between Isla San José and Isla Cocinero (10°51′50″N, 86°55′30″W), Islas Murciélago, Provincia Guanacaste, 3–11 m depth, 17 February 1972, 1 shell, leg. P. LaFollette, D. Cadien, and A. Ferreira (LACM 72-21.20). Bahía Potrero Grande (10°50′56″N, 85°48′35″W), Provincia Guanacaste, 9–10 m depth, 17 February 1972, 5 shells, leg. P. LaFollette and A. Ferreira (LACM 72-29.13). South tip of Punta Santa Elena (10°53′35″N, 85°57′52″W), Provincia Guanacaste, 12–15 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-30.27). 5 miles north west of Islas Huevos (10°41′45″N, 85°46′25″W), Golfo de Papagayo, Provincia Guanacaste, 60–64 m depth, 18 February 1972, 1 shell, leg. P. LaFollette and D. Cadien (LACM 72-34.30). Middle of Bahía Huevos, north of Bahía Culebra (10°38′41″N, 85°41′55″W), Provincia Guanacaste, 10–23 m depth, 18–19 February 1972, 11 shells, leg. P. LaFollette and D. Cadien (LACM 72-35.45). Off beach at Bahía Brasilito (10°25′57″N, 85°49′18″W), Provincia Guanacaste, 18 m depth, 20 February 1972, 46 shells, leg. P. LaFollette and D. Cadien (LACM 72-40.36). 1.5 mile east of Punta Ballena (9°44′15″N, 84°33′45″W), Provincia Guanacaste, 3–15 m depth, 21–22 February 1972, 4 shells, leg. P. LaFollette and D. Cadien (LACM 72-42.62). Anchorage at Bahía Ballena off Tambor (10°44′10″N, 84°59′34″W), Provincia Puntarenas, 10 m depth, 21 February, 1972, 30 shells, leg. P. LaFollette and A. Ferreira (LACM 72-43.19). Off beach at Bahía Ballena (9°44′12″N, 84°59′32″W), Provincia Puntarenas, 3–18 m depth, 23 February 1972, 4 shells, leg. P. LaFollette and D. Cadien (LACM 72-45.42). Bahía Herradura (9°38′45″N, 84°40′55″W), Provincia Puntarenas, 9–17 m depth, 9–10 March 1972, 4 shells, leg. J. McLean (LACM 72-52.63). Bahía Herradura (9°37′58″N, 84°40′30″W), Provincia Puntarenas, 21 m depth, 9 March 1972, 31 shells, leg. J. McLean (LACM 72-53.30). Off Bahía Herradura (9°38′50″N, 84°40′50″W), Provincia Puntarenas, 37 m depth, 10 March 1972, 30 shells, leg. J. McLean (LACM 72-54.57). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22′43″N, 84°09′41″W), Provincia Puntarenas, 21 m depth, 11 March 1972, 29 shells, leg. J. McLean (LACM 72-57.41). Small islets off Punta Quepos (9°22′43″N, 84°09′41″W), Provincia Puntarenas, 9–23 m depth, 11–13 March 1972, 3 shells, leg. J. McLean (LACM 72-58.59). Small islets off Punta Quepos (9°22′12″N, 84°09′15″W), Provincia Puntarenas, 23 m depth, 12 March 1972, 2 shells, leg. J. McLean (LACM 72-59.31). North side of Isla del Caño (8°43′15″N, 83°53′07″W), Provincia Puntarenas, 7–14 m depth, 14–19 March 1972, 26 shells, leg. J. McLean and D. Wheeler (LACM 72-63.81). Isla del Caño (8°44′00″N, 83°52′30″W), Provincia Puntarenas, 12 m depth, 14–19 March, 1972, 27 shells, leg. J. McLean (LACM 72-64.19). 1.5 km northwest of Playa Junquillal (10°58′40.7139N, 85°42′27.2867W), Provincia Guanacaste, 20 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003501383). Manuel Antonio National Park (9°22′36.6614N, 84°09′23.2807W), Provincia Puntarenas, 15–20 m depth, 1 specimen, 17 February 2003, leg. F. González (INB0003575268). Isla David (10°56′06.0000N, 85°42′53.0000W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 18 m depth, 4 shells, 12 March 1996, leg. R. Angulo (INB0003575678). Isla David (10°56′06.0000N, 85°42′53.0000W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 18 m depth, 6 shells, 12 March 1996, leg. R. Angulo (INB0003575681). National Park Manuel Antonio (9°22′36.6614N, 84°09′23.2807W), Provincia Puntarenas, 15–20 m depth, 4 shells, 17 February 2003, leg. F. González (INB0003707722). La Viuda Rock (8°36′56.0065N, 83°14′08.0868W), Golfo Dulce, Provincia Puntarenas, 66 m depth, 21 April 1997, 1 shell, leg. M. Lobo (INB0003722832). Boca de Estero Caballero (8°40′06.3050N, 83°26′41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 1 shell, leg. M. Lobo (INB0003747045). Playa Mostrencal

(10°59′47.3060N, 85°42′53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 1 shell, 13 March 1996, leg. R. Angulo (INB0003747048). Playa Mostrencal (10°59′47.3060N, 85°42′53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 3 shells, 13 March 1996, leg. R. Angulo (INB0003747334). Playa Mostrencal (10°59′47.3060N, 85°42′53.8890W), Bahía Junquillal, Golfo Santa Elena, Provincia Guanacaste, 2 m depth, 3 shells, 13 March 1996, leg. R. Angulo (INB0003747410). Isla David (10°58′05.5000N, 85°42′38.6000W), Bahía Junquillal, Santa Rosa National Park, Provincia Guanacaste, 30 m depth, 12 March 1996, 3 shells, leg. Y. Camacho (INB0003747596).

Shell morphology.— Length up to 5 mm; width up to 2 mm in the largest specimen examined. Shell fragile, elongate, with convex sides, much wider in the central area (Fig. 10A–B). Only one whorl visible, except for a visible portion of the top of the spire. Apex umbilicated with the aperture lip conspicuously rising from the left side, forming a rounded wing connected to the columellar margin. Anterior end of the shell elongate. Umbilicus wide and deep. Aperture long, wider anteriorly, narrowing at about ⅓ of its length and widening again near the apex. Columella with a single, conspicuous fold. Sculpture with several spiral grooves near the anterior and posterior ends of the shell, absent from the middle area. Color uniformly dirty white.

Anatomy.— Digestive system with a gizzard containing three irregular gizzard plates. Each plate with a series of transverse, parallel ridges composed of small, simple denticles (Fig. 10C). All plates similar in shape and size. Radular formula 10 × 3.1.3 in a specimen from Manuel Antonio (INB0003575268). Lateral teeth hook-shaped with a long and strong cusp bearing numerous denticles (Fig. 10D). Rachidian teeth broad, with a wide triangular base and a broad central cusp bearing numerous small denticles.

Remarks.— The shell morphology of the specimens here examined is identical to the original description of *Cylichnella defuncta* by Baker and Hanna (1927). This species was originally described in the genus *Cylichnella* and subsequently transferred to *Acteocina* by Skoglund (2002), based on the synonymization of *Cylichnella* with *Acteocina* by Mikkelsen and Mikkelsen (1984).

However, the anatomy of *Cylichnella defuncta* is very different from those of *Acteocina* and *Cylichnella*. The gizzard plates have a series of transverse, parallel ridges composed of small, simple denticles, and the radula has broad rachidian teeth, with a wide triangular base and a broad central cusp bearing numerous small denticles as well as hook-shaped lateral teeth with a long and strong cusp bearing numerous denticles. All these anatomical features as well as the shell morphology, characterized by the presence of striae near the posterior and anterior ends of the shell and the outer lip clearly rising over the apex, are typical of the genus *Atys*. Therefore *C. defuncta* is here regarded as a member of *Atys*.

Family Bullidae Gray, 1827

Genus *Bulla* Linnaeus, 1758

Bulla punctulata A. Adams in Sowerby, 1850

(Figs. 7B, 10E–G, 11)

Bulla punctata A. Adams in Sowerby, 1848–50 [1850]:577, pl. 123, fig. 77 (non Bulla punctata Schroeter, 1804).

Bulla punctulata A. Adams in Sowerby, 1848–50 [1850]:604.

Type material.— *Bulla punctata*: Syntypes (2): Panama (BMNH 19760047).

Material examined.— Playa Ocotal, Provincia Guanacaste, 14 May 1976, 8 shells, leg. A. Hardy and R. Hardy (CASIZ 048833). Puerto Culebra, Provincia Guanacaste, 1 shell (CASIZ 017943). Cove on northwest side of Isla San Pedrito (10°51′30″N, 86°57′57″W), Islas Murciélago, Provincia Guanacaste, 2–4 m depth, 17 February 1972, 1 juvenile shell, leg. P. LaFollette and D. Cadien (LACM 72-22.13). Islas Tortugas,

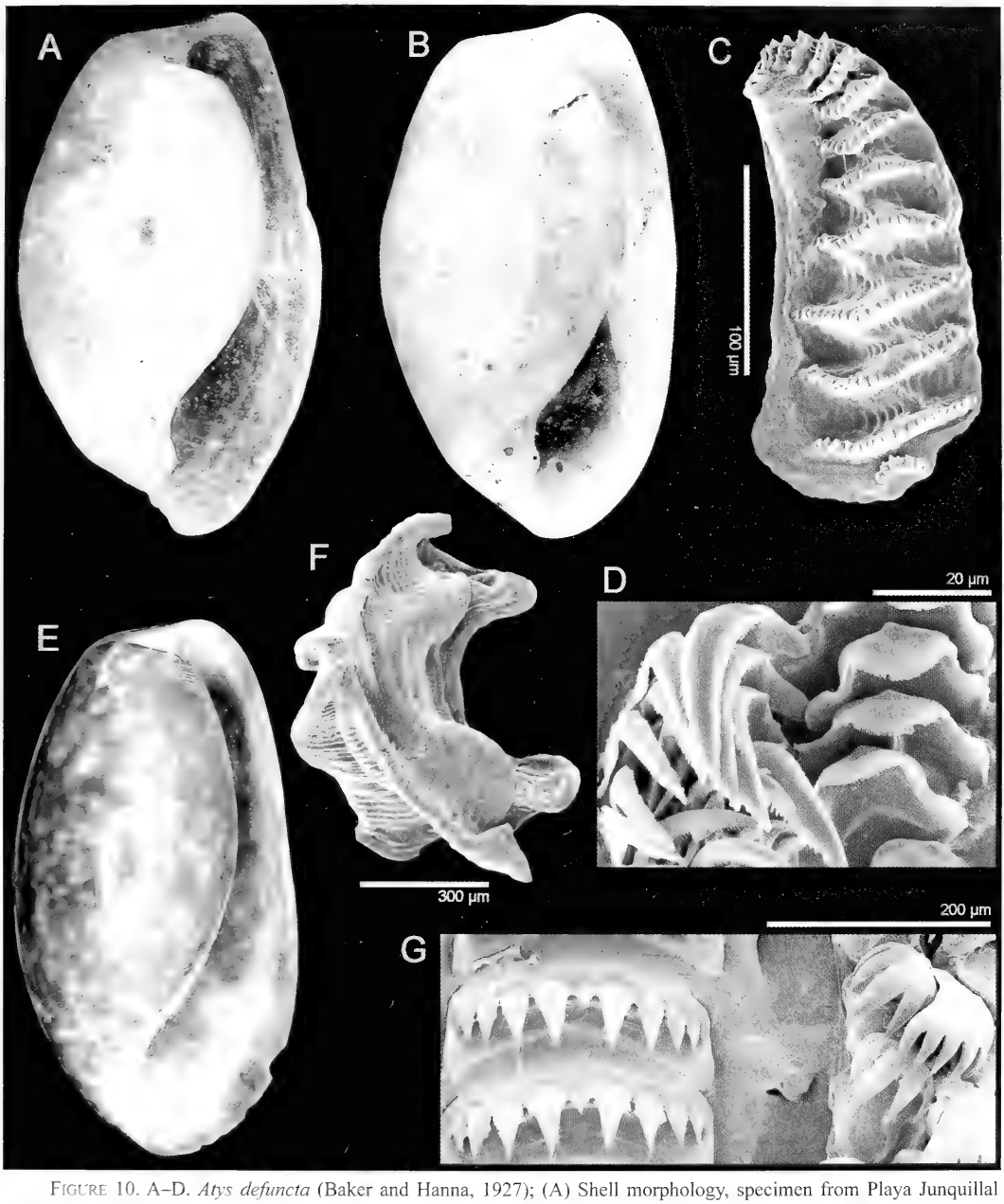

FIGURE 10. A–D. *Atys defuncta* (Baker and Hanna, 1927); (A) Shell morphology, specimen from Playa Junquillal (INB0003501383); 3 mm long; (B) Shell morphology, specimen from Parque Nacional Manuel Antonio, (INB0003575268) 3 mm long; (C) Gizzard plate, same specimen; (D) Radular teeth, same specimen. E–G, *Bulla punctulata* A. Adams in Sowerby, 1850; (E) Shell morphology, specimen from Golfo Dulce (INB0003540757), 7.5 mm long; (F) Gizzard plate, specimen from Isla Bolaños and Playa Coyotera (INB0003502783); (G) Radular teeth, same specimen.

Provincia Puntarenas, 2–8 m depth, 23–24 February 1972, 7 shells, leg. P. LaFollete, D. Cadien, and A. Ferreira (LACM 72-46.59). Anchorage inside of small islet 1.5 km south of Punta Quepos (9°22′43″N, 84°09′41″W), Provincia Puntarenas, 21 m depth, 11 March 1972, 4 juvenile shells, leg. J. McLean (LACM 72-57.42). Isla del Caño (8°44′00″N, 83°52′30″W), Provincia Puntarenas, 12 m depth, 14–19 March, 1972, 1 juvenile shell, leg. J. McLean (LACM 72-64.20). Boca del Estero Caballero (8°40′06.3050N, 83°26′41.8580W), Provincia Puntarenas, 0 m depth, 11 June 1995, 1 shell, leg. M. Lobo (INB0001499756). Murciélago (10°58′14.7752N, 85°42′04.1162W), Provincia Guanacaste, 20 m depth, 5 specimens, 6 April 2002, leg. F. González (INB0003461244). 200 m northwest of Playa Guaria (10°57′55.1620N, 85°42′23.7922W), Bahía Junquillal, Provincia Guanacaste, 8 m depth, 4 April 2002, 1 shell, leg. F. González (INB0003500963). Bahía Tomás (10°55′44.7444N, 85°43′15.9105W), Murciélago, Provincia Guanacaste, 1 m depth, 3 juvenile shells, 9 April 2002, leg. F. González (INB0003501262). Bahía Tomás (10°55′44.7444N, 85°43′15.9105W), Murciélago, Provincia Guanacaste, 1 m depth, 2 shells, 9 April 2002, leg. F. González (INB0003501266). Between Isla Bolaños and Playa Coyotera (11°02′51.0971N, 85°43′21.1040), Bahía Salinas, Provincia Guanacaste, 12 m depth, 10 April 2002, 2 specimens, leg. F. González (INB0003502783). 1 km west of Playa Junquillal (10°58′24.5393N, 85°42′04.1590W), Bahía Junquillal, Provincia Guanacaste, 30 m depth, 5 April 2002, 5 shells, leg. F. González (INB0003504311). Between Playa Palma and Playa Bejuco (8°43′10.6630N, 83°25′19.9570W), Golfo Dulce, Provincia Puntarenas, 0 m depth, 8 November 1996, 1 shell, leg. M. Lobo (INB0003540757). Bahía Santa Elena (10°54′48.0420N, 85°48′18.5810W), Provincia Guanacaste, 0 m depth, 4 shells, 16 February 1994, leg. G. Bassey (INB0003542096). Isla Ballena (9°06′18.0003N, 83°43′42.7017W), Provincia Puntarenas, 18 m depth, 18 January 2003, 1 specimen, leg. S. Ávila (INB0003572555).

Shell morphology.— Length up to 7 mm; width up to 5 mm in the largest specimen examined. Shell solid, oval, with convex sides (Fig. 10E). Only one whorl visible, forming the entire shell. Apex rounded, deeply umbilicated, with the aperture lip rising from the left side. Anterior end of the shell rounded. Umbilicus absent. Aperture long, wide anteriorly, narrowing gradually at about ⅓ of its length, and continuing posteriorly as a narrow canal. Columellar margin thickened. Surface smooth and shiny. Sculpture reduced to fine growth lines, except for the areas near the anterior and posterior ends of the shell, with several conspicuous spiral lines. Color reddish brown, scattered with irregular white and black blotches. Columella white.

External morphology.— Body is oval, 9 mm long in the largest specimen examined. Cephalic shield short, comprising about ⅙ of the body length (Fig. 7B). Each side of the head with an involute lateral extension. Hancock's organs composed of 7 simple folds. Posterior ⅚ of the body almost entirely covered by the shell. Gill simple, composed of 15 unipinnate lamellae. Color of the living animals pale brown, with numerous small white spots. Shell completely opaque.

Anatomy.— Buccal bulb oval to elongate, connected posteriorly to the short esophagus and the long salivary glands (Fig. 11A). Esophagus opening into a large gizzard, which contains three smooth and irregular gizzard plates (Fig. 10F), all of them similar in shape and size. Plates conical, with four ridges and

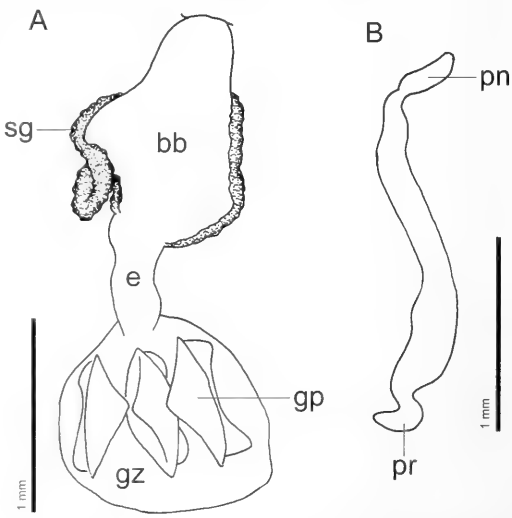

Figure 11. *Bulla punctulata* A. Adams in Sowerby, 1850, anatomy of specimen from Isla Bolaños and Playa Coyotera (INB0003502783); (A) Anterior portion of the digestive system; (B) Male reproductive system. Abbreviations: bb, buccal bulb; e, esophagus; gp, gizzard plate; gz, gizzard; pn, penis; pr, prostate; sg, salivary gland.

longitudinal striations on the inner side. Radular formula 21 × 2.1.2 in a specimen from Bahía de Salinas (INB0003502783). Lateral teeth wide, with a short base and 5 sharp cusps (Fig. 10G). Rachidian teeth broad, short, with a small, triangular central cusp and four larger denticles on each side of the cusp.

Reproductive system monoaulic. Penis small, connecting to the prostate through a long and convoluted duct (Fig. 11B).

Geographic range.— Reported in the eastern Pacific from Peru to Baja California, Mexico (Skoglund 2002).

Remarks.— The specimens here examined have similar shell morphology to the two syntypes of *Bulla punctulata* and there is no doubt they belong to the same species.

Family Aglajidae Pilsbry, 1895

Genus *Aglaja* Renier, 1807

Aglaja regiscorona Bertsch, 1972

(Fig. 12A–B)

Aglaja regiscorona Bertsch, 1972:103–104, fig 1.

Type material.— *Aglaja regiscorona*: Holotype: Bahía Las Cruces, Baja California del Sur, México (CASIZ 024043); Paratypes: Bahía Las Cruces, Baja California del Sur, México, three specimens (LACM 1617).

Material examined.— San Miguel, Reserva Natural Absoluta de Cabo Blanco, Provincia Puntarenas, 2 m depth, 16 May 1998, 1 specimen, leg. A. Berrocal (INB0001498365); SW of Isla Plata, Provincia Guanacaste, 10 m depth, 17 April 2004, 1 specimen, leg. Y. Camacho (INB0003836172).

Shell morphology.— Length 1 mm; width 0.5 mm in the single specimen examined. Shell calcified with a distinct whorl, a curved apical border, and a broad flat wing (Fig. 12B). Protoconch globose, about 2 whorls, 200 μm in diameter.

External morphology.— Body elongate, 5 mm long in the specimen examined. Cephalic shield triangular, projecting posteriorly and upwards into a small, three pointed crown (Fig. 12A). Parapodia small, not extending over the dorsal surface. Posterior end of the body with two big lobes lacking a flagellum. Color of the living animal cream white. Dorsum and cephalic shield covered with numerous papillae, speckled with black. Parapodia and posterior lobes with several small black spots.

Geographic range.— Known only from Bahía Las Cruces, Baja California Sur (Skoglund 2002) and Costa Rica (present paper).

Remarks.— *Aglaja regiscorona* was originally described from Baja California based on several specimens collected from Bahía Las Cruces (Bertsch 1972). An examination of the type material has confirmed that the specimen from Costa Rica belongs to the same species. The shell morphology of this species is described here for the first time.

Genus *Navanax* Pilsbry, 1895

Navanax aenigmaticus (Bergh, 1894)

(Fig. 7C)

Navarchus aenigmaticus Bergh, 1894:217, pl. 10, figs. 11–12, pl. 11, figs. 6–9, pl. 12, figs. 8–10.

Type material.— Untraceable.

Material examined.— Bahía Alcyone, Cocos Island, 34 m depth, 25 March 1989, 1 specimen, leg.

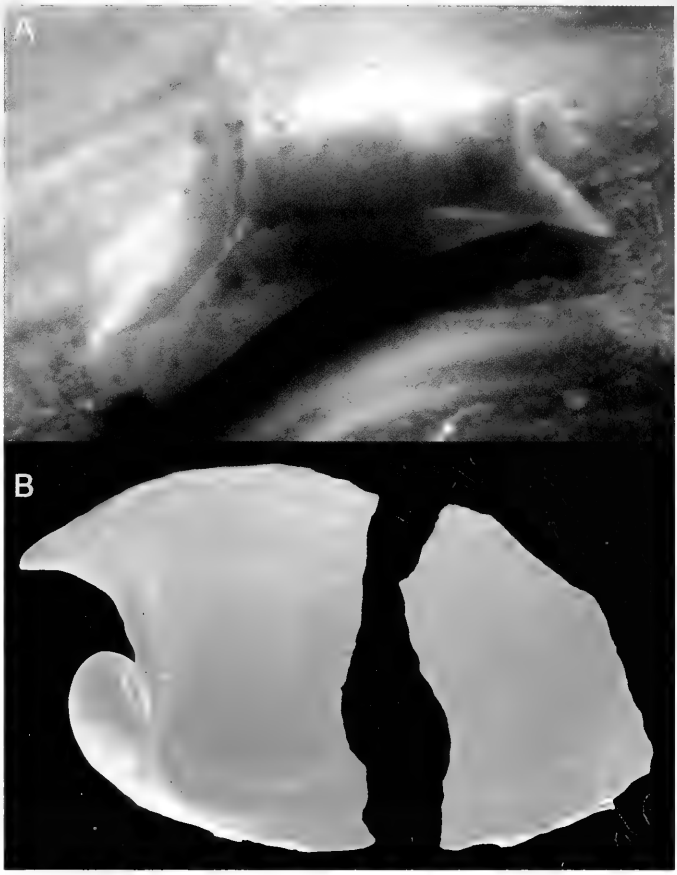

FIGURE 12. *Aglaja regiscorona* Bertsch, 1972, specimen from Cabo Blanco (INB0001498365); (A) Living animal; (B) Shell morphology, 1 mm long (complete).

K. Kaiser (CASIZ 073370). North side of Isla del Caño (8°43′15″N, 83°53′07″W), Provin-cia Puntarenas, 0 m depth, 18–19 March 1972, 1 specimen, leg. J. McLean (LACM 72-68.44). Bahía Junquillal, Sector SE (10°57′55 .2170N, 85°42′07.2810 W), Parque Nacional Santa Rosa, Provincia Guanacaste, 1 m depth, 9 December 1995, 1 specimen, leg. Y. Camacho (INB0001486933). Playa Grande (10°20′59.1902N, 85°51′55.8818 W), 500 m W from Punta Carbón, Provincia Guanacaste, 0 m depth, 11 January 2001, 2 specimens, leg. S. Avila (INB0003118189). Playa San Miguel (9°34′45.8380N, 85°08′8 .6800W), Reserva Natural Absoluta de Cabo Blanco, Provincia Punt arenas, 2 m depth, 30 April 1995, 1 specimen, leg. G. Mena (INB000 1498434). Playa Manzanillo (9°56′03.4990N, 84°54′52.7660W), Isla Golfo de San Lucas, Provincia Puntarenas, 2 m depth, 9 December 1999, 2 specimens, leg. M. Calderón (INB0001496008). Estación San Miguel (9°34′53.9500N, 85°08′28 .5380W), Reserva Natural Absoluta de Cabo Blanco, Provincia Punt arenas, 0 m depth, 28 January 1999, 1 specimen, leg F. Alvarado (INB0001495820). Punta Uvita (9°08′44.4580N, 83°45′33.2680W), Parque Nacional Marino Ballena, Provincia Puntarenas, 0 m depth, 15 January 2000, 2 specimens, leg. M. Calderón (INB0001496175). Punta Uvita (9°08′50.9650N, 83°45′47.1900W), Parque Nacional Marino Ballena, 0 m depth, 13 April 1996, 6 specimens, leg. S. Avila (INB0001486546). East Side of Isla Ballena (9°06′24.5090N, 83°43′35.8230W), Parque Nacional Marino Ballena, Provincia Puntarenas, 6 m depth, 16 January 2000, 1 specimen, leg. M. Calderón (INB0001495898). 500 meters South of Playa Ventanas (9°05′16.1660N, 83°40′50.7600W), Provincia Puntarenas, 0 m depth, 17 January 2000, 1 specimen, leg. M. Calderón (INB0001495974). San Pedrillo (8°36′53.6350N, 83°44′18.3791W), Parque Nacional Corcovado, Provincia Puntarenas, 0 m depth, 20 January 2000, 1 specimen, leg. M. Calderón (INB0001495989). San Pedrillo (8°36′40.6143N, 83°44′16.7412W), Provincia Puntarenas, 0 meters depth, 21 January 2000, 1 specimen, leg. M. Calderón (INB0001495985). San Pedrillo (8°37′22.9440N, 83°44′18.3830W), Parque Nacional Corcovado, Provincia Puntarenas, 0 m depth, 27 February 1998, 8 specimens, leg. A. Berrocal (INB0001498380). San Pedrillo (8°37′00.1590N, 83°44′11.8370W), Parque Nacional Corcovado, Provincia Puntarenas, 0 m depth, 19, 1 specimen, leg. A. Berrocal (INB0001496543). 100 m SE of Punta Curupacha (8°37′57.8040N, 83°13′14.0600W), Provincia Puntarenas, 7 m depth, 29 January 1998, 3 specimens, leg. A. Berrocal (INB0001498379). Roca Negritas (9°12′58.2630N, 83°50′14.2490W), Provincia Puntarenas, 0 m depth, 17 May 1995, 2 specimens, leg. M. Madrigal (INB0001482914). Rock in front Cabo Matapalo (8°22′17.3370N, 83°17′31.7800W), Península de Osa, Provincia Puntarenas, 18 m depth, 13 February 1997, 1 specimen, leg. S. Avila (INB0001498367).

Cambutal (9°13′21.0780N, 83°50′22.4180W), Provincia Puntarenas, 0 m depth , 16 May 1995, 3 specimens, leg. Y. Camacho (INB0001485355). Punta Voladera, from the tower to NE (8°37′25.8910N, 83°10′56.7300W), Reserva de Vida Silvestre Golfito, Provincia Puntarenas, 0 m depth, 8 May 1997, 2 specimens, leg. M. Madrigal (INB0001498405). Punta Gallardo (8°37′35.0910N, 83°14′16.2310W), Parque Nacional Piedras Blancas, Puntarenas Provincia, 10 m depth, 6 March 1997, 1 specimen, leg. S. Avila (INB0001498361).

External morphology.— The body is very elongate, 30 mm long, in the specimens examined. The cephalic shield is also elongate, comprising about ½ of the body length (Fig. 7C). The two Hancock's organs are composed of about 16 simple folds. There are large sensory processes at each side of the mouth opening. The parapodia are narrow. The posterior shield is rounded posteriorly, with two broad lobes similar in size and shape. The gill is simple, with 11 groups of lamellae. The color of the living animals is pale brown with irregular large brown spots that vary in position and size. There is a series of bright blue spots on each side of the head and along the edge of the parapodia.

Geographic range.— Widespread in the tropical and subtropical eastern Pacific and Atlantic. In the Pacific it ranges from Southern Mexico to Chile (Skoglund 2002).

Remarks.— The systematics of *Navanax aenigmaticus* has been investigated by Gosliner (1980), who provided a complete list of synonyms. Gosliner (1980) also provided illustrations of the anatomy and shell morphology of the species, so that information is not repeated here.

Navanax polyalphos (Gosliner and Williams, 1972)

(Figure 13A–C)

Chelidonura polyalphos Gosliner and Williams, 1972:424–436.

Type material.— *Chelidonura polyalphos*: Holotype: Bahía San Carlos, 6 km north of Guaymas, Sonora, México (CASIZ 549).

Material examined.— 500 m W of Punta Carbón, Playa Grande, Provincia Guanacaste, 0 m depth, January 11, 2001, 1 specimen, leg. S. Avila (INB0003118180); South side of Punta Zapotal, Provincia Guanacaste, 8–10 m depth, April 15, 2004, 1 specimen, leg. T.M. Gosliner (INB0003836138).

Shell morphology.— Length 2.5 mm; width 1.25 mm, in the single specimen examined. Shell calcified with a distinct wing-like structure protruding from the body whorl. The inner edge of the wing is thickened (Fig. 13). The protoconch is globose, about 1.5 whorl, 200 μm in diameter. Color yellowish brown.

External morphology.— The body is elongate, 5–20 mm long, in the specimens examined. The anterior end of the body has two grooved lobes. The eyes are large and are visible on the dorsal surface of the cephalic shield. The posterior end of the body terminates in two long acute "tails." The cephalic shield covers the anterior and pharyngeal region of the animal while the posterior shield covers the mantle and posterior viscera. The color of the living animals is dark brown, almost black, and generally with two rows of bright blue spots near the inner side of the parapodia. There are numerous small whitish spots, larger and more numerous in some areas of the dorsal surface. Often, these spots are aggregated to form patches on the shields. In some specimens there are also some small yellowish spots.

Geographic range.— Known from the Channel Islands in southern California to Panama.

Remarks.— Gosliner and Williams (1972) provided a complete description of this species including illustrations of the reproductive and nervous system and shell morphology of the species, so that information is not repeated here.

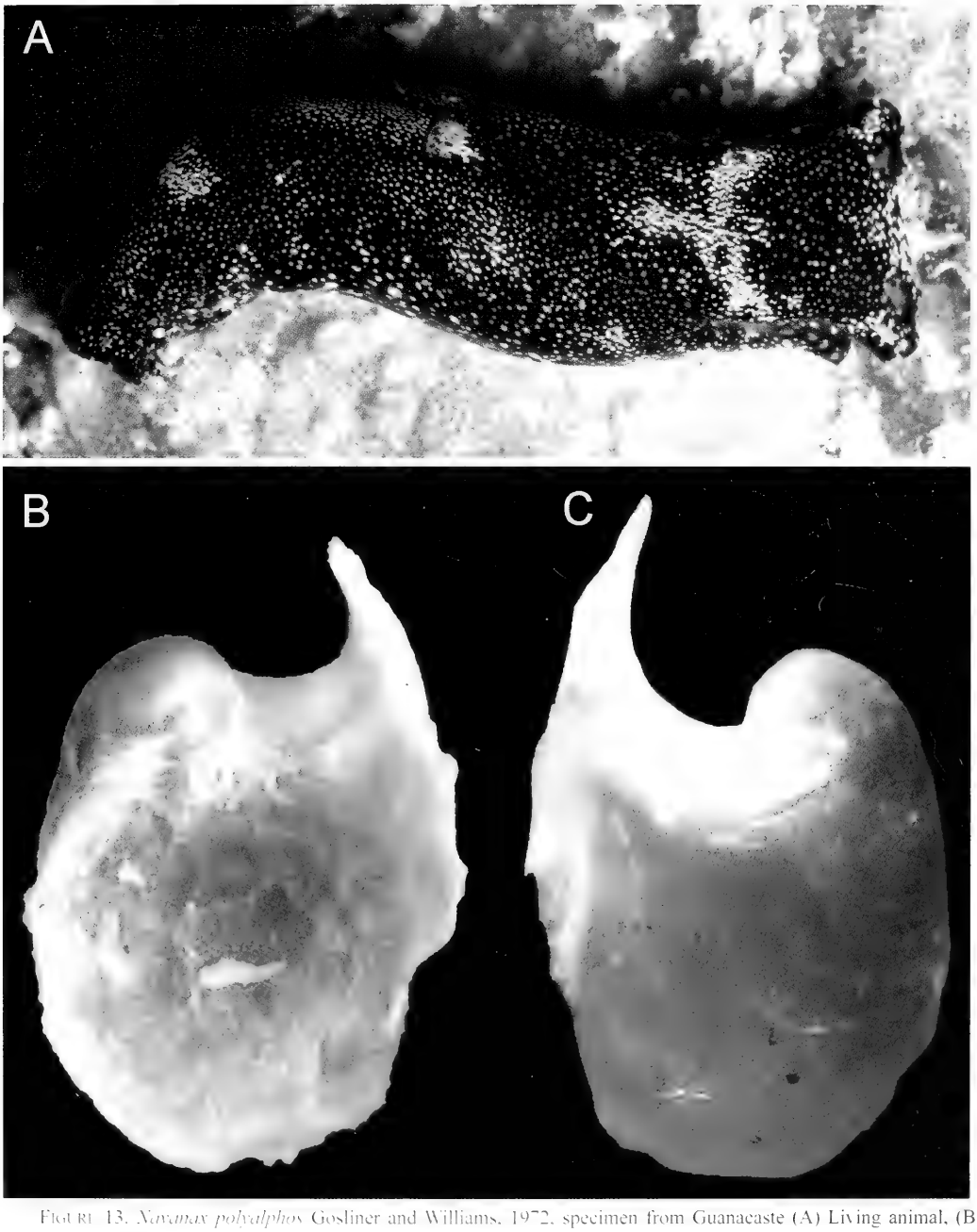

FIGURE 13. *Navanax polyalphos* Gosliner and Williams, 1972, specimen from Guanacaste (A) Living animal, (B) Detail of the ventral side of the shell, 2.5 mm long, (C) Detail of the dorsal side of the shell, 2.5 mm long.

Acknowledgments

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The Marine Gobies of the Hawaiian Islands

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A total of 34 species of gobies (Teleostei, Gobiidae) are known from the Hawaiian Islands, four of which are freshwater species. All species are treated in a key, but only marine species are illustrated and treated in detail. Information on their nomenclature, counts and measurements, distinctive characters, coloration, distribution and habitat is presented. Two new species, *Cabillus caudimacula*, and *Pleurosicya larsonae* are described. An unidentified species of *Favonigobius* from O'ahu, a possible introduction, is discussed.

The Gobiidae is the largest family of marine fishes, with many species also occurring in fresh water. J.S. Nelson (pers. commun., September 2003) estimates that there are about 220 genera and 2010 species. Judging from the number of undescribed species of gobies of which we are aware, that number of species will surely be exceeded.

Most gobies are small (the shortest goby is *Trimmatom nanus*, with females maturing at as little as 8 mm standard length; but one species, *Glossogobius giuris*, attains 500 mm standard length). Gobies generally are recognized by their pelvic-fin structure; the fins usually are fused to form a sucking disc which may have an anterior transverse membrane called a frenum that links the spines. When the pelvic fins are separate, they are close together. Gobies and sleepers (family Eleotridae) have been confused in the past, and some gobies with separate pelvic fins have been misidentified as sleepers. Gobies have five branchiostegal rays, whereas the sleepers have six, and the pelvic fins are more broadly separated than in the gobies with the pelvic fins divided. All Hawaiian gobies normally have six spines in the first dorsal fin, except for *Discordipinna griessingeri* with five. Most gobies, and all in Hawaiian waters, also usually have two separate dorsal fins.

The Hawaiian Islands have a total of 34 species of gobies, four of which (*Awaous guamensis*, *Lentipes concolor*, *Sicyopterus stimpsoni*, and *Stenogobius hawaiiensis*) are fresh water. In 1905, Jordan and Evermann recognized eight marine gobies in the Hawaiian Islands. Gosline and Brock (1960) found 13. As a result of collecting since then, the number is now 30. These 30 marine species occur in salt to brackish water from tidepools high in the splash zone to moderate depths. One species was recently taken by trawl in 138–169 m. Although some gobies, such as species of the genus *Bathygobius*, can readily be seen scurrying around tidepools, most are secretive and not easily observed. They are, however, an important part of the communities in which they are present. In a survey of the fishes of Kâne'ohe Bay, Greenfield (2003) found that the most abundant species taken in collections using an ichthyocide was the goby *Eviota epiphanies*. In reference to species of *Eviota*, Greenfield and Randall (1999) wrote "These small gobies may form an important component of the food of larger piscivorous fishes." Other gobies, of course, also serve as prey to larger fishes.

Although all species are treated in our key, only the marine species are included in this paper. Several small individuals of a goby species in the genus *Favonigobius* were taken at Kahana Bay, O'ahu, but were too small to be identified (see Discussion).

Materials and Methods

All counts and measurements follow Hubbs and Lagler (1964) except that the last two rays of the dorsal and anal fins are not counted as one unless it is clear that they are joined at the base. Measurements were made to the nearest 0.1 mm using dial calipers, and are expressed as percentages of standard length (SL). Lengths given in figure captions of specimens are standard length (SL), but for underwater photographs, the length is the estimated total length (TL). In the descriptions of the new species, measurement data for the holotype are presented first, followed by the range and mean (in parentheses) for all type material. For other descriptions the count or measurement is followed by the mode or mean, respectively, in parentheses. Color descriptions are from 35-mm slides taken under water of either living individuals or ones recently collected, or fresh specimens out of water. When listing type material for various species, often only those at the Bernice P. Bishop Museum in Honolulu (BPBM) are listed. Institutional abbreviations are as listed in Leviton et al. (1985).

Key to the Gobies of Hawaii

1a. Pelvic fins separate, inner rays of both fins not connected (Fig. 1.) 2
1b. Pelvic fins fused to form a sucking disc, or at least inner rays of both fins connected together (membrane is easily torn, may only be joined at bases of fins) (Fig. 2). 5

2a.(1a) Preopercle with two or more spines (Fig. 3); pelvic fins not fringe-like, lacking many side branches . . . . . *Asterropteryx semipunctatus*
2b.(1a) Preopercle without spines; pelvic fin with many side branches and fringe-like (Fig. 4) 3

3a.(2b.) Unbranched 5th pelvic-fin ray not developed (Fig. 4); genital papillae of male and female not ruggose (Fig. 5); subcutaneous dark-brown bar at caudal-fin base (Fig. 6); anteriormost branch of 4th pelvic-fin ray short, with fewer than 10 segments; IT pore present (Fig. 7) . . . . . *Eviota epiphanes*
3b.(2b) Unbranched 5th pelvic-fin ray developed (about 1/10 length of 4th ray) (Fig. 8); genital papillae of male and female ruggose (Figs. 9 and 10); no subcutaneous bar at caudal-fin base; anteriormost branch of 4th pelvic-fin ray elongate, with 9 or more segments (usually about 15) (Figs. 8 and 11); IT pore absent (Fig. 7) 4

4a(3b) No prominent subcutaneous body bars or spots; POP pores present (Fig. 7); size to 12.8 mm SL. . . . . *Eviota rubra*
4b(3b) Five-6 prominent subcutaneous body bars, ventral surface with 3 broad subcutaneous bars on belly and 4–6 more spots above anal-fin base and on caudal peduncle (Fig. 12); POP pores absent or greatly reduced (Fig. 7); size to 18.5 mm SL . . . . . *Eviota susanae*

5a.(1b) Caudal fin distinctly forked (young of various freshwater gobies) . . . *Vitraria clarescens*[3]
5b.(1b) Caudal fin rounded or pointed 6

[3] *Vitraria clarescens* in literature, a synonym of *Sicyopterus stimpsoni* (Greenfield et al. 1998).

6a.(5b) Caudal fin distinctly pointed, more than twice as long as wide (Fig. 13); a well-developed fleshy crest on nape extending forward from first dorsal fin at least past edge of opercle and further in larger specimens (Fig. 14) 7
6b.(5b) Caudal fin rounded, not twice as long as wide; no distinct median crest on nape 8

7a.(6a) Body with lateral series of elongate blotches; dark spot on superior margin of eye; prominent dark spot on pectoral-fin base (Fig. 14); dark spots on branchiostegal membranes under lower jaw (Fig. 15); 18–21 (usually 20) pectoral-fin rays. . . . . *Oxyurichthys lonchotus*
7b.(6a) Body lacking elongate blotches on sides, spots on eye margin, pectoral-fin base, or branchiostegal membranes; 21–23 (usually 22–23) pectoral-fin rays . . . . . *Oxyurichthys heisei*

8a.(6b) Upper 4–9 pectoral-fin rays terminating in free, silky filaments (Fig.16). 9
8b.(6b) Upper pectoral-fin rays not terminating in free, silky filaments 11

9a.(8a) Pelvic sucking disc about as wide as long (Fig. 17); anterior nostril with a small flap; side of cheek with a deep longitudinal groove, with upper portion of cheek extending down over groove anteriorly, hiding papillae in groove (Fig. 18); predorsal scales extending forward to between eyes; upper 8–10 pectoral-fin rays with free, silky filaments . *Bathygobius cotticeps*
9b.(8a) Pelvic sucking disc clearly longer than wide (Fig. 19); no flap on anterior nostril; side of cheek with a shallow groove anteriorly, with papillae present in groove visible; predorsal scales not extending forward to between eyes; upper 4–6 pectoral-fin rays with free, silky filaments. 10

10a.(9b) Predorsal scales extending forward of a line drawn up from posterior edge of preopercle, almost to eyes in some (in specimens 28 mm SL and larger); mandibular frenum straight with no free lobes at sides (Fig. 20). . . . . *Bathygobius coalitus*
10b.(9b) Predorsal scales not extending forward to line drawn up from posterior edge of preopercle; mandibular frenum more curved with free lobes at sides (Fig. 21) . . . . . *Bathygobius cococensis*

11a.(8b) Lateral scales on back anterior to second dorsal fin smaller than those under second dorsal fin and on caudal peduncle (Fig. 23); interorbital area covered with very small cirri (Fig. 22); no pores on top of head . . . . . *Mugilogobius cavifrons*
11b.(8b) Size of scales (if present) not obviously different between anterior and posterior parts of body; interorbital area lacking small cirri; pores on top of head present or absent 12

12a.(11b) About three prominent, knob-like, fleshy projections extending forward from lower portion of shoulder girdle inside gill openings (Fig. 24).(freshwater species). 13
12b.(11b) No knob-like, fleshy projects on shoulder girdle. 14

13a.(12a) A black blotch extending down and back from eye; caudal fin not crossed by any dark bars (fresh water) . . . . . *Stenogobius hawaiiensis*
13b.(12a) No black blotch under eye; caudal fin crossed by about 5 dark bars (fresh water) . . . . . *Awaous guamensis*

14a.(12b) Origin of first dorsal fin far forward on body, above posterior end of operculum and with five spines; second dorsal-fin spine greatly elongate, extending well back above second dorsal fin . . . . . *Discordipinna griessingeri*
14b.(12b) Origin of first dorsal fin behind origin of pectoral fin and with six spines; second dorsal-fin spine may be elongate or not 15

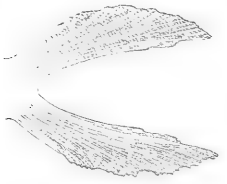

FIGURE 1. Pelvic fins of *Asterropteryx semipunctatus*.

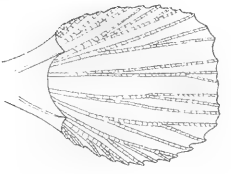

FIGURE 2. Pelvic fins of *Bathygobius coalitus*.

FIGURE 3. Head of *Asterropteryx semipunctatus*.

FIGURE 4. Pelvic fin of *Eviota epiphanes*.

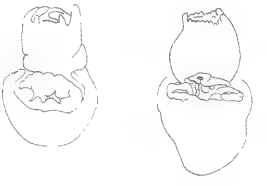

FIGURE 5. Genital papillae of *Eviota epiphanes*, male on left.

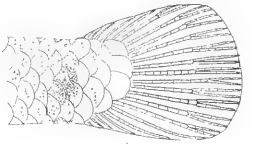

FIGURE 6. Caudal peduncle and fin of *Eviota epiphanes*.

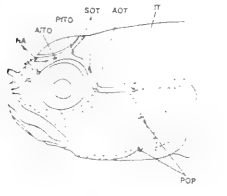

FIGURE 7. Cephalic pores of *Eviota* species, modified from Lachner and Karnella (1980).

FIGURE 8. Pelvic fin of *Eviota rubra*.

FIGURE 9. Genital papillae of *Eviota rubra*, male on right.

FIGURE 10. Genital papillae of *Eviota susanae*, male on right.
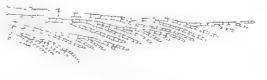
FIGURE 11. Pelvic fin of *Eviota susanae*.

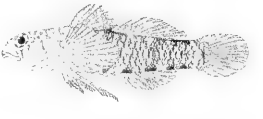

FIGURE 12. *Eviota susanae*.

FIGURE 13. Caudal fin of *Oxyurichthys lonchotus*.

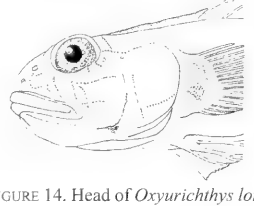

FIGURE 14. Head of *Oxyurichthys lonchotus*.

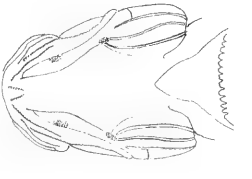

FIGURE 15 Ventral view of head of *Oxyurichthys lonchotus*.

FIGURE 16. Pectoral fin of *Bathygobius coalitus*.

FIGURE 17. Pelvic fins of *Bathygobius cotticeps*.

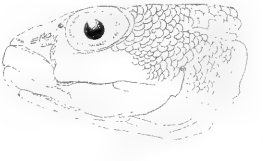

FIGURE 18. Head of *Bathygobius cotticeps*.

15a.(14b) Pelvic fins with a frenum that is thickened and variously raised, thickened portion with a folded pocket in the center extending back onto disc (probe may be inserted into pocket at anterior part of disc) (Fig. 25) 16

15b.(14b) Pelvic fins with or without a frenum, but if present not thickened and raised (usually a thin membrane); no folded pocket in frenum 22

16a.(15a) Interorbital wide, about one and one-half to two eye diameters; snout broadly rounded from side view (Fig. 26); pelvic-fin frenum lacking pelvic-spine lobes or short papillae . . 17

16b.(15a) Interorbital narrow, less than one eye diameter; snout more pointed from side view (Fig. 27); pelvic-fin frenum with thickened skin around pelvic spines, forming lobes that extend posteriorly over disc (lobes may be less distinct, but if so, are covered with many, short papillae) (Figs. 28–29) 18

17a.(16a) Scales on body extending forward onto head (fresh water) . . . . . *Sicyopterus stimpsoni*

17b.(16a) Body naked or with a few scales on posterior part of body near caudal peduncle (fresh water) . . . . . *Lentipes concolor*

18a.(16b) Interorbital very narrow, about ½ pupil diameter; a single pore in center of interorbital (Fig. 30) 19

18b.(16b) Interorbital wider, slightly narrower than one pupil diameter; two pores in center of interorbital, one next to each eye (Fig. 31) 20

19a.(18a) Pelvic-fin frenum with two distinct lobes of thickened skin around pelvic spines, extending posteriorly over disc; frenum not broad and covered with short papillae (Fig. 28); dark pigment on lower portion of caudal peduncle extending posteriorly as stripe onto caudal fin . . . . . *Pleurosicya micheli*

19b.(18a) Pelvic-fin frenum broader, lobes not as distinct and frenum covered with short papillae (Fig. 32): body peppered with melanophores, no distinct dark stripe on caudal peduncle and caudal fin . . . . . *Pleurosicya larsonae*

20a.(18b) Pectoral-fin rays 13 (rarely 12 or 14); a distinct black stripe from eye forward onto snout . . . . . *Bryaninops tigris*

20b.(18b) Pectoral-fin rays 14–17 (rarely 13); stripe from eye to snout absent or if present indistinct 21

21a.(20b) Scalloped grooves present along lower edge of preoperculum (Fig. 33); head depth 50% or more of head length; body bars golden brown to brown when live, generally distinct in preserved material . . . . . *Bryaninops yongei*

21b.(20b) No scalloped grooves present along lower preopercular edge (occasionally slight indentations along margin); head depth less than 50% of head length; body bars brownish-orange to red when live; usually indistinct in preserved material . . . . . *Bryaninops amplus*

22a.(15b) Body naked, with about 10–11 dark vertical bars separated by narrow white bars; pelvic disc short, space between posterior end of fin and anal-fin origin equal to or greater than pelvic-fin length . . . . . *Kelloggella oligolepis*

22b.(15b) Body with scales, at least posteriorly; body without 12 dark vertical bars; pelvic disc longer, space between posterior end of pelvic fin and anal-fin origin clearly less than pelvic-disc length 23

23a.(22b) Gill membranes broadly fused to isthmus; gill opening not extending anteriorly as far as posterior edge of preopercle 24

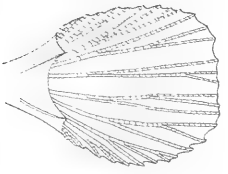

FIGURE 19. Pelvic fins of *Bathygobius coalitus*.

FIGURE 20. Ventral view of head of *Bathygobius coalitus*.

FIGURE 21. Ventral view of head of *Bathygobius cocosensis*.

FIGURE 22. Back of *Mugilogobius cavifrons*.

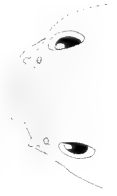

FIGURE 23. Dorsal view of head of *Mugilogobius cavifrons*.

FIGURE 24. Pectoral-fin base of *Awaous guamensis*.

FIGURE 25. Pelvic fins of *Sicyopterus stimpsoni*.

FIGURE 26. Head of *Sicyopterus stimpsoni*.

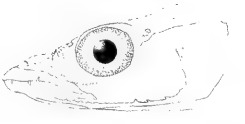

FIGURE 27. Head of *Bryaninops amplus*.

FIGURE 28. Pelvic fins of *Pleurosicya micheli*.

FIGURE 29. Pelvic fins of *Bryaninops yongei*.

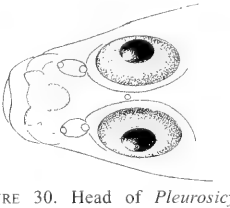

FIGURE 30. Head of *Pleurosicya micheli*.

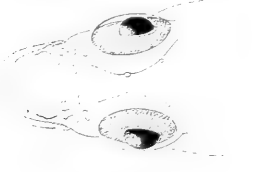

FIGURE 31. Head of *Bryaninops amplus*.

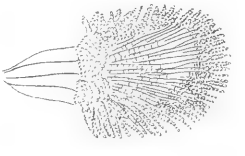

FIGURE 32. Pelvic fins of *Pleurosicya larsonae*.

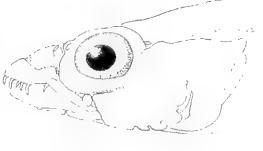

FIGURE 33. Head of *Bryaninops yongei*.

FIGURE 34. Head of *Gnatholepis anjerensis*.

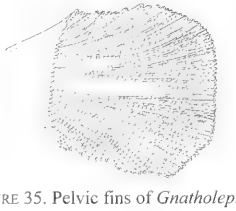

FIGURE 35. Pelvic fins of *Gnatholepis anjerensis*.

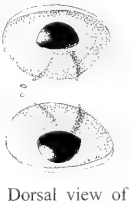

FIGURE 36. Dorsal view of eyes of *Gnatholepis anjerensis*.

23b.(22b) Gill membranes not broadly fused to isthmus, gill openings extending forward to or beyond posterior edge of preopercle 27

24a.(23a) Narrow black bar extending down from under eye across cheek and under head (Fig. 34); pelvic-fin frenum well-developed and obvious, extending to near ends of pelvic-fin spines (Fig. 35) 25
24b.(23a) No narrow black bar under eye; pelvic-fin frenum weak, thin and often not obvious, and not extending to near ends of pelvic-fin spines 26

25a.(24a) Pectoral-fin rays 15–17 (modally 16, rarely 15); a narrow dark bar dorsally on eye, centered over posterior half of pupil, not crossing interorbital space (Fig. 36); small scales usually present on cheek anterior to dark eye bar; size to 64 mm SL ..... *Gnatholepis anjerensis*
25b.(24a) Pectoral-fin rays 16–18 (modally 17, rarely 16 or 18); narrow dark bar dorsally on eye, centered at pupil, often crossing midinterorbital space (Fig. 37); small scales rarely present on cheek entirely anterior to dark eye bar; size to 42 mm SL
..... *Gnatholepis cauerensis hawaiiensis*

26a.(24b) Head about as deep as wide; snout pointed (Fig. 38); small dark spot at center of caudal-fin base (Fig. 39); no scales with enlarged cteni at caudal-fin base . *Coryphopterus duospilus*
26b.(24b) Head much wider than deep; snout more rounded (Fig. 40); large dark spot covering most of caudal-fin base; two large scales with enlarged cteni at top and bottom of caudal-fin base (Fig. 41) ..... *Cabillus caudimacula*

27a.(23b) Posterior end of jaws extending to or past posterior margin of eye; top of head lacking scales; pelvic-fin frenum very well-developed, extending posteriorly one-third to one-half length of fin (Fig. 42). ..... *Psilogobius mainlandi*
27b.(23b) Posterior end of jaws not reaching posterior margin of eye; top of head with at least some scales from front of dorsal fin forward; pelvic-fin frenum absent or less developed, not extending posteriorly one-third length of fin 28

28a.(27b) Gill opening extending forward to near posterior edge of preopercle 29
28b.(27b) Gill opening extending forward to at least midway between posterior edge of preopercle and eye 32

29a.(28a) Head with a series of prominent, dark-bordered light lines radiating out from eye across cheek and top of head (Fig. 43); anal fin with one spine and 7 rays; midline of nape naked anterior to dorsal fin ..... *Priolepis farcimen*
29b.(28a) Head without a series of prominent, dark-bordered lines; anal fin with one spine and 8 or more rays; midline of nape with scales anterior to dorsal fin 30

30a.(29a) Scales present on cheek and opercle (Fig. 44); a deep interorbital trench present between eyes (Fig. 45); fins generally dark ..... *Priolepis eugenius*
30b.(29a) Cheek and opercle lacking scales; interorbital without a trench; fins not dark 31

31a.(30b) Scales on body with dark borders (Fig. 46); second dorsal fin with 9 rays; anal fin with 8 to 9 rays, usually 8; predorsal scales 5 to 8; longitudinal scale series 24–26, usually 25
..... *Priolepis limbatosquamis*
31b.(30b) Scales on body lacking dark borders; second dorsal fin with 11–12 rays, usually 11; anal fin with 9–10 rays, usually 9; predorsal scales 12–16, usually 15; longitudinal scale series 28–30, usually 28 ..... *Priolepis aureoviridis*

32a.(28b) Gill opening extending forward only to posterior margin of eye; first spine in second part

FIGURE 37. Dorsal view of eyes of *Gnatholepis cauerensis hawaiiensis*.

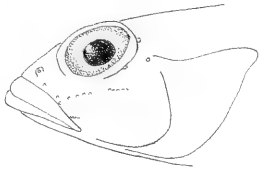

FIGURE 38. Head of *Coryphopterus duospilus*.

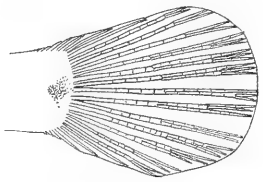

FIGURE 39. Caudal peduncle and fin of *Coryphopterus duospilus*.

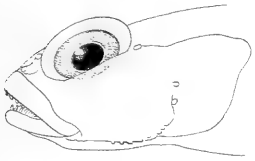

FIGURE 40. Head of *Cabillus caudimacula*.

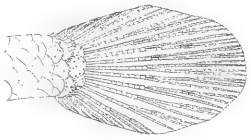

FIGURE 41. Caudal peduncle and fin of *Cabillus caudimacula*.

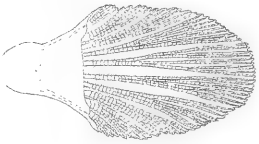

FIGURE 42. Pelvic fins of *Psilogobius mainlandi*.

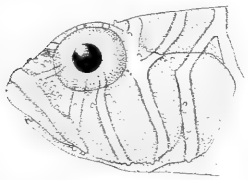

FIGURE 43. Head of *Priolepis farcimen*.

FIGURE 44. Head of *Priolepis eugenius*.

FIGURE 45. Dorsal view of head of *Priolepis eugenius*.

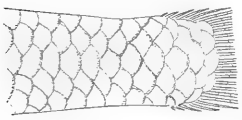

FIGURE 46. Scales on side of body of *Priolepis limbatosquamis*.

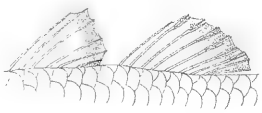

FIGURE 47. Dorsal fins of *Trimma unisquamis*.

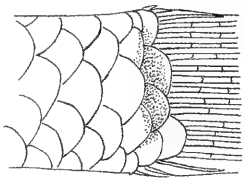

FIGURE 48. Caudal-fin base of *Trimma unisquamis*.

of dorsal fin stout and sharp-tipped; body with a line of dash-like dark marks down side and several fainter lines above. . . . . *Opua nephodes*

32b.(28b) Gill opening extending far forward to under chin and anterior part of eye; first spine in second part of dorsal fin not stout and sharp-tipped; series of dash-like marks not present on side of body 33

33a.(32b) Both dorsal fins with a black border , more obvious in first (Fig. 47); a dark band at base of caudal fin (Fig. 48); dorsal-fin spines not elongate. . . . . *Trimma unisquamis*

33b.(32b) Dorsal fins without black borders; no dark band at base of caudal fin; dorsal-fin spines may or may not be elongate. 34

34a.(33b) Bony interorbital narrow, less than half pupil diameter; pectoral-fin rays 17–18; second dorsal spine not prolonged; soft dorsal rays 9, soft anal rays 8. . . . . *Trimma milta*

34b.(33b) Bony interorbital wider, about equal to pupil diameter; pectoral-fin rays 13–15; second dorsal spine long and filamentous (may reach caudal-fin base in males); soft dorsal rays 10–11, soft anal rays 9–10. . . . . *Trimma taylori*

Asterropterix semipunctatus Rüppell, 1830

(Figs. 3 and 49)

Asterropterix semipunctatus Rüppell, 1830, Fische Rothen Meeres 1828–30:138, pl. 34, fig. 4. Red Sea. Holotype: SMF 1691.

Brachyeleotris cyanostigma Bleeker, 1855, Nat. Tijdschr. Ned. Indië 8:452. Cocos-Keeling Is., Indian Ocean. Syntypes: RMNH 4756(2).

FIGURE 49. *Asterropteryx semipunctatus*, 50 mm TL, Kâne'ohe Bay, O'ahu.

DIAGNOSIS.— Counts based on 20 individuals, 24.0–34.6 mm SL. Dorsal-fin elements VI-I,10. Anal-fin elements I,8-I,9 (I,9). Pectoral-fin rays 17–19 (18). Longitudinal scale series 24–25 (24). Pelvic fins separate, without numerous fringe-like side branches. Lower part of preopercle with two or more spines. Scales ctenoid, covering body; head scaled except interorbital space, snout, and chin. Gill membranes broadly united to isthmus; gill opening ending under middle of opercle. Mouth oblique, lower jaw protruding; jaws extending past anterior margin of eye but not to pupil. Small conical teeth in bands in jaws, the outer row at the front enlarged. Interorbital narrow, about equal to pupil diameter. Third dorsal spine prolonged to a long filament in large adults. Caudal fin rounded, shorter than head. Body depth 3.0–3.6 in standard length. Reported to 65 mm TL.

COLOR IN ALCOHOL.— Male- Background color either light cream or medium brown. Light color morph: body with five longitudinal stripes from head back to caudal-fin base, one at midline, two above, and two below. A dark brown spot at top of pectoral-fin base. Caudal-fin base with dark-brown bar. Top of caudal peduncle dark brown. Head with small dark-brown spot at posteriodorsal margin of eye. A diffuse light-brown bar from anteroventral margin of eye to posterior end of jaws. A dark bar on chin from mandible to mandible. Pectoral fins clear. Pelvics, caudal, anal, and second part of dorsal fin with scattered melanophores. First part of dorsal fin with a dark-brown spot at posterior portion. Dark-color morph: basic color pattern as for light morph except less distinct because of dark background. Pectoral fins with scattered melanophores. Other fins as in light morph except more melanophores and thus darker. Female- Color the same as dark-color morph of male.

LIVE COLOR.— (from photograph taken at Kâne'ohe Bay) Background color gray with pattern of black markings, entire body overlaid by small, iridescent blue spots. Body crossed by six, irregular, black saddles that extend down to ventral surface: First from top of pectoral-fin base up to origin of first dorsal fin; second from base of posterior half of first dorsal fin; third from elements three to seven of second dorsal fin; fourth from last few rays of second dorsal fin and onto caudal peduncle; fifth at middle of caudal peduncle; and sixth at caudal-fin base. Ventral surface at anal-fin base black, joining bases of saddles together. A separate black blotch extending up from anal-fin origin to midline between saddles two and three. Nape and top of head mottled black and gray, lower half of side of head black. Pupil of eye black surrounded by a narrow golden ring, remainder of iris mottled black and gray. Pectoral-fin base black except for a gray patch at center that extends out onto fin-ray bases; remainder of fin dusky. Pelvic, anal, and caudal fins dusky. First

dorsal fin dusky with alternating black and gray bars on spines. First spine of second dorsal fin with alternating black and gray bars, remainder of fin dusky.

Distribution.— Throughout most of the Indo-Pacific region from the Red Sea and Indian Ocean to the Society Islands and Hawaiian Islands.

Remarks.— Usually lives in shallow protected waters of bays and lagoons, often on dead reefs (Greenfield, 2003). Classified in the earlier literature as an eleotrid because of the divided pelvic fins. Privitera (2001, 2002) studied its reproductive biology in the Hawaiian Islands. Spawning occurs at various times during the day, year-around, with a peak from May to July. Clutch size varied from 296–1552 (mean 886), independent of length of the female. Eggs are ellipsoidal and varied from 0.67–0.84 mm in length, hence unusually small for a body of this size. Eggs were laid beneath coral; they were tended by the male who periodically fanned them with its pectoral fins. Eggs hatched in laboratory aquaria shortly after lights were turned off, four to six nights after being deposited in the nest. Newly hatched larvae had a mean notochord length of 1.88 mm. Minimum age at maturity, 17.5–19 mm, estimated as four and one-half to five months after hatching. Also known as the bluespotted goby.

Material examined.— Hawaiian Islands: O'ahu: CAS 218097 (10), CAS 218089 (10), BPBM 5471 (7), BPBM 22621 (10), BPBM 37315 (9), BPBM 37316 (3); Hawai'i: 28719 (6); Midway Atoll: BPBM 35370 (6).

Bathygobius coalitus (Bennett, 1832)

(Figs. 2, 16, 19–20, and 50)

Gobius coalitus Bennett, 1832, Proc. Zool. Soc. London 1830–31(pt 1):166. Mauritius. Holotype: BMNH 1856.2.15.20.

Figure 50. *Bathygobius coalitus*, 50 mm TL, Maui Ocean Center.

Diagnosis.— Counts based on 26 individuals, measurements on 10 individuals 40.2–77.6 mm SL. Dorsal-fin elements V-VI-I,8-9 (VI-I,9). Anal-fin elements I,7-I,9 (I,8). Pectoral-fin rays 18–20 (19), the upper 4–6 (5) rays filamentous, branched to base with membrane-free ends. Longitudinal scale series 34–37 (36). Predorsal scales 15–20. Pelvic sucking disc longer than wide, space between end of fin and anal-fin origin less than one fin length; broad frenum with an obvious spine on each side of frenum pointing posteriorly. Body covered with ctenoid scales, becoming cycloid on abdomen, chest, and nape; extending forward on head past a line drawn up from posterior edge of preopercle, almost to eyes in some individuals. No scales on opercle or cheek. Gill membranes broadly united to isthmus. Jaws extending posteriorly to mid-pupil. Interorbital narrow, about equal to pupil diameter. No flap on anterior nostril. Side of cheek with a shallow groove anteriorly, with papilla in groove visible. Mandibular frenum straight with no free lobes at sides. Caudal fin rounded, about equal to head length. Head depressed, its width greater than its depth. Body depth 4.3–4.7 in standard length. Reported to 120 mm TL.

Color in alcohol.— Head and body light cream. Upper half of body with four dark brown saddles: First from fourth spine of dorsal fin posterior to just past end of fin base and down to meet mid-side blotches; second saddle from third element of second dorsal fin posterior to base of seventh element and down to meet mid-side blotches; third saddle from base of last element posterior

onto three scales of caudal peduncle and down to meet mid-side blotches; last saddle covering last two scales of caudal peduncle prior to caudal fin and down to meet mid-side blotches; first and third saddles darkest and most prominent. Midside of body with a series of about eight to nine interconnected dark brown blotches that do not reach ventral surface of body. Dark area on top of head immediately in advance of first dorsal-fin spine. Head with four dark brown blotches around eye: one, the most prominent, posterior to orbit at level of top of opercle; second anterior to this; third at posteroventral margin of orbit; fourth at anteroventral margin of orbit extending onto premaxilla; two additional dark brown blotches posterior to most prominent spot posterior to orbit, first midway between eye and top of opercle and second at top of opercle. A distinct dark brown spot on middle of opercle adjacent to edge of preopercle. Cheek with mottled pattern. Eye with clear pupil and black iris. Pectoral fin covered with scattered melanophores, a distinct spot present at bases of rays 6–8 and a second more diffuse spot over bases of rays 12–15. Anal fin with scattered melanophores, darker on distal ⅔ of membranes. Caudal fin of female with dark brown blotch at center of base and then crossed by four to five indistinct bars. Caudal fin of male with dark brown blotch at base, proceeded by light area containing two blotches. A circle of dark spots out past ½ of fin length. Fin posterior to this with one dark bar and then generally dusky. First part of dorsal fin covered with melanophores concentrated into dark spots on basal half of membranes between spines four to six. Second part of dorsal fin crossed by six bars angling dorsoventrally across fins. Pelvic fins covered with melanophores in males, fewer in females.

Color of fresh specimen.— (from photograph of specimen collected at Kâne'ohe Bay) Background color golden brown with dark brown to gray mottled pattern scattered over body, darker on back, nape, top and sides of head. Body with scattered, small, white spots, some arranged into irregular rows. Side of head with many scattered, small, white spots. Ventral surface of head and body white with scattered peppering of melanophores, isthmus with dark gray blotches. Eye with black pupil and iris dark brown with an orange tinge. Pelvic fins white with a peppering of melanophores. Caudal-fin membranes dusky, rays dark brown with white spots on basal three-quarters. Anal fin dusky with dark gray distal margin. Pectoral-fin membranes dusky, rays brown with white spots on basal one-half. First dorsal fin with rows of white spots along base with a narrow dark brown bar distal to spots. Another row of white spots above brown bar. Middle third of fin dusky with additional row of white spots. Distal third of fin membrane clear with an orange margin. Second dorsal fin similar to first dorsal fin.

Distribution.— East coast of Africa to the Hawaiian Islands and Marquesas; Japan to the Great Barrier Reef.

Remarks.— Typically found in the intertidal zone in rock and tidepools. Shafer (1998) reported that this species spawns throughout the year, has a larval duration of 29–50 days, settles at 7.02–10.6 mm total length, and reaches its maximum size in 20–30 days.

Material examined.— Hawaiian Islands: O'ahu: CAS 218099 (13), uncataloged, (G91-11), CAS 218100- (3), CAS 218099 (13); BPBM 5490 (1), BPBM 34559 (1); Hawai'i: BPBM 34622 (2); Necker: BPBM 4863 (1).

Bathygobius cocosensis (Bleeker, 1854)

(Figs. 21 and 51)

Gobius cocosensis Bleeker, 1854, Nat. Tijdschr. Ned. Indië 7:47. Cocos-Keeling Islands, Indian Ocean. Holotype: lost. Neotype: RMNH 4533, selected by Akihito and Megura (1980); location of neotype unknown.

Mapo fuscus: Jordan and Evermann, 1905, Bull. U.S. Fish Comm. 23(1):483, fig. 212 (misidentification).

Diagnosis.— Counts based on 25 individuals, measurements on 10 individuals 28.5–56.3 mm

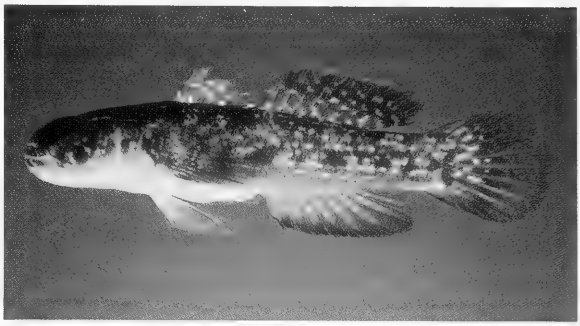

FIGURE 51. *Bathygobius cocosensis*, BPBM 33489, 41 mm SL, Kâne'ohe Bay, O'ahu.

SL. Dorsal-fin elements VI-I,7-VI-I,10 (VI-I-9). Anal-fin elements I,7-I,9 (I,8). Pectoral-fin rays 17–20 (18), the upper 4–6 (5) rays filamentous, branched to base with membrane-free ends. Longitudinal scale series 34–38 (35). Predorsal scales 10–12. Pelvic sucking disc longer than wide, space between end of fin and anal-fin origin less than one fin length; broad frenum with an obvious spine on each side of frenum pointing posteriorly. Body covered with ctenoid scales, becoming cycloid on abdomen, chest, and nape; scales extending forward on head to a line drawn up from posterior edge of opercle. No scales on opercle or cheek. Gill membranes broadly united to isthmus. Jaws extending posteriorly to posterior margin of pupil. Interorbital narrow, about equal to pupil diameter. No flap on anterior nostril. Side of cheek with a shallow groove anteriorly, with papillae in groove visible. Mandibular frenum curved with free lobes at sides. Caudal fin rounded, about equal to head length. Head depressed, its width greater than its depth. Body depth about 5 in standard length. Reported to 60 mm TL.

COLOR IN ALCOHOL.— Head and body light cream; upper half of body with four dark brown saddles, first from third spine of dorsal fin posterior to just past end of fin base and down to meet midside blotches; second saddle from second element of second part of dorsal fin posterior to base of 6th element and down to meet midside blotches; third saddle from base of 8th element posterior onto three scales of caudal peduncle and down to meet midline blotches; last saddle covering last two scales of caudal peduncle prior to caudal fin down to meet midline blotches. Midside of body with a series of about eight to nine interconnected dark brown blotches that do not reach ventral surface of body. Dark area on top of head immediately in advance of first dorsal spine, resembling a saddle. Head with a prominent dark brown blotch posterior to orbit at level of top of opercle; a second spot posterior to this spot midway between eye and top of opercle, third spot at top of opercle. An additional spot on posteroventral margin of orbit. A diffuse dark brown spot on middle of opercle adjacent to edge of preopercle. Pectoral fin covered with scattered melanophores, with no distinct spots. Anal fin evenly covered with melanophores. Caudal fin of female crossed by seven distinct bars. Caudal fin and first and second dorsal fins of males evenly covered with melanophores. First dorsal fin of female crossed by four bars angling dorsoventrally across fin. Second dorsal fin of female crossed by six similar bars.

COLOR OF FRESH SPECIMEN.— (from photograph of specimen taken at Kâne'ohe Bay) Background color golden brown with dark brown mottled pattern scattered over body, darker on top of back by first dorsal fin, nape, top and sides of head. Body with about five irregular rows of small, white spots from pectoral-fin base to caudal-fin base. Ventral surface of head and body white with scattered peppering of melanophores. Side of head with scattered small, white spots. Eye with black pupil and iris dark brown, lips gray with white spots. Pelvic fins white basally, remaining two-thirds dusky. Caudal fin dark brown with white spots on basal one-third of rays, rays darker than membranes. Anal-fin membranes light gray on basal two-thirds, distal one-third dark brown. Pectoral fin dark brown with small, white spots on basal one-half. First dorsal fin with a peppering of melanophores, crossed by three rows of white spots, distal margin orange. Basal half of second dorsal fin with a peppering of melanophores, distal half dark brown, fin crossed by four to five rows of white spots.

Distribution.— Widespread throughout the tropical Indo-Pacific region.

Remarks.— Typically found in tidepools, shallow reef flats, and sheltered patch reefs. Often misidentified in recent literature (including Gosline and Brock, 1960) as *B. fuscus* (Rüppell).

Material examined.— Hawaiian Islands: O'ahu: CAS 218101 (12), CAS 218102 (13), CAS 218103 (28), CAS 218104 (3), CAS 218105 (16), CAS 218106 (19), CAS 218107 (4) BPBM 5483 (49), BPBM 5486 (23), BPBM 5488 (43).

Bathygobius cotticeps (Steindachner, 1879)

(Figs. 17–18 and 52)

Gobius cotticeps Steindachner, 1879, Sitzungsber. Akad. Wiss. Wien. 80(1 Abth.):137. Society Islands. Holotype: NMW 30439.

Chlamydes laticeps Jenkins, (1903), Bull. U.S. Fish. Comm. 22(1902):503, Fig. 43, O'ahu , Hawaiian Islands. Holotype: USNM 50716.

Figure 52. *Bathygobius cotticeps*, BPBM 38464, 57 mm SL, Waikîkî, O'ahu.

Diagnosis.— Counts based on 25 individuals, measurements on 10 individuals 27.8–57.8 mm SL. Dorsal-fin elements VI-I,8-I,9 (VI-I,9). Anal-fin elements I,7-I,8 (I,8). Pectoral-fin rays 21—25 (24), upper 8–10 (9) rays filamentous, branched to based with membrane-free ends. Longitudinal scale series 35–39 (37). Predorsal scales 21–32. Pelvic sucking disc about as wide as long, moderately long, space between end of fin and anal-fin origin less than one fin length; broad frenum with an obvious spine on each side of frenum pointing posteriorly. Body covered with ctenoid scales, becoming small and cycloid on head and anterior body, extending forward onto head to between eyes, onto upper portion of opercle and onto cheek under eye in larger individuals. Gill membranes broadly united to isthmus. Jaws extending posteriorly to anterior part of pupil. Interorbital narrow, about equal to pupil diameter. Anterior nostril with a small flap. Side of cheek with a deep longitudinal groove, with upper portion of cheek extending down over groove anteriorly, hiding papillae in groove. A small fleshy lobe projecting posteriorly from front of chin, without a posterior projection on each side. Caudal fin rounded, shorter than head. Head strongly depressed. Body depth 4.2–5.0 in standard length. Reported to 110 mm TL.

Color in alcohol.— Head and body light cream. Body crossed by four brown saddles: first from second spine of first dorsal fin posterior past end of fin base to end of depressed last spine and down to belly; second saddle from first ray of second part of dorsal fin posterior to base of 5th ray and down to midline of body where it joins third saddle; third saddle from base of 7th ray posterior about two scales past end of fin base and down to midline of body; posterior third of third saddle extends posteroventrally to end of last depressed anal-fin ray on ventral surface of caudal peduncle; fourth saddle encircles caudal peduncle just anterior to caudal-fin base. Head with a dark bar extending posteroventrally from posterior part of ventral surface of eye across cheek ⅔ distance to edge of preopercle; second shorter bar extending from anteroventral portion of eye onto premaxilla; distinct round spot at posterior edge of eye, second spot posterior to this spot midway between eye and top of opercle, third spot at top of opercle. Pectoral fin with scattered melanophores on basal ⅔. Anal fin with scattered melanophores on basal ¾. Caudal fin crossed by six faint bars composed of separate spots on fin rays. First part of dorsal fin with a dark spot covering membrane between spines five and six continuing past sixth spine to end of fin. Second part of dorsal fin crossed by six faint bars angling dorsoventrally across fin. Pelvic fin lacking pigment.

Color of fresh specimen.— (from photograph of specimen taken at Waikîkî). Background color medium brown with dark brown edges on scales on sides of body and head, entire scales dark brown on dorsal surface of body and head. Ventral surface of head and body white with scattered melanophores. Eye with black pupil, iris brown with gold reflections. Grooves on cheek cream, contrasting with darker background of cheek. Lips dark brown. Pectoral, anal, and caudal fins uniform dark brown to gray. Pelvic fins tan. First dorsal fin with a clear area on basal one-fifth between spines two and six. Remainder of fin darker, spines orange-brown and membranes dusky brown, an intense black spot between spines five and six and extending slightly posterior to sixth spine. Second dorsal-fin membranes dusky brown, spine and rays orange-brown.

Distribution.— Found in the Indo-Pacific from East Africa to the Hawaiian Islands and Pitcairn Islands; in the western Pacific from Japan to the Great Barrier Reef.

Remarks.— Usually found in tidepools and rocky shores. This species is more abundant in the low intertidal, in areas that do not get cut off from the ocean during low tide (D.J. Shafer, pers. commun., March 1998)

Material examined.— Hawaiian Islands: O'ahu: BPBM 4869 (2), BPBM 5492 (1), BPBM 5493 (3), BPBM 5494 (2), BPBM 11659 (3), BPBM 15354 (8), BPBM 15370 (7), CAS 218109 (2), CAS 218165 (1); uncat. Univ. Hawaii (2), uncat. Univ. Hawaii (2), Univ. Hawaii 2018 (4).

Bryaninops amplus Larson, 1985

(Figs. 27, 31, and 53)

Bryaninops amplus Larson, 1985, The Beagle (Occ. Pap. N. Terr. Mus. Arts Sci.) 2(1):66, figs. 5–6. Lagoon off east tip of Palfrey I., Lizard I., Great Barrier Reef, Australia. Holotype: AMS I.22916-001. Paratypes: BPBM 27979 (1), Hawai'i, BPBM 29319 (9), Hawai'i, other paratypes at various museums.

Diagnosis.— Counts based on two individuals 23.9–25.2 mm SL. Dorsal-fin elements VI-I, 8. Anal-fin elements I,9. Pectoral-fin rays 15. Longitudinal scale series 46–49. Body variably scaled, the scales extending forward to between end of pectorals and below fourth dorsal-fin spine, abdomen naked. Snout pointed and bill-like, longer than eye diameter. A large curved canine tooth at midside of lower jaw. Gill opening reaching ventrally a little below pectoral-fin base. Pelvic sucking disc slightly longer than wide, but short, space between posterior end of fin and anal-fin origin greater than pelvic-fin length. Pelvic-fin frenum with thickened skin around pelvic spines, forming lobes that extend posteriorly over disc. Interorbital slightly narrower than one pupil diameter with two pores in center of interorbital, one next to each eye. No scalloped grooves along lower preopercular edge. Head depth less than 50% of head length. Body depth at anal-fin origin 6.2–9.0 in standard length. Caudal fin slightly emarginated to truncate with rounded corners. No dark bars on back. Reported to 56 mm TL.

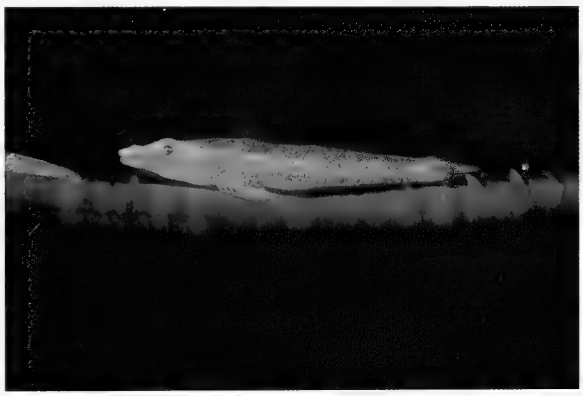

Figure 53. *Bryaninops amplus*, 45 mm TL, on seawhip, Kaua'i.

Color in alcohol.— Background color light cream. Body with a few scattered melanophores on back with slight concentrations in front of first dorsal fin, between spines five and six, at first three elements of second dorsal fin, at fifth ray of second dorsal fin, behind second dor-

sal fin, and at end of caudal peduncle. Lower half of body with heavier concentration of melanophores, becoming more dense towards caudal-fin base and extending onto basal one-third of caudal fin. Remainder of caudal fin without pigmentation. Top of head with scattered, larger dark brown spots. Cheek and opercle with a few scattered melanophores and a heavy concentration of melanophores on anterior end of upper and lower jaws. Pectoral-fin base with scattered melanophores, no pigmentation on fin. Both dorsal fins, anal and pelvic fins lack pigmentation.

Color in life.— (from a photograph taken at 21 m at Kaua`i) Body translucent with most apparent color showing through from internal pigmentation. Internal coloration: A bright white line running along backbone. Area below backbone dark brown with two distinct white bars running across gut area from backbone to ventral surface. A series of about eight bright white spots spaced on ventral portion of body above anal-fin base. Red gills show through side of head, inner surface of eye balls and brain white. External coloration: An orange-red stripe extending the length of body just ventral to backbone. Six evenly spaced, orange-red triangles extending dorsally from stripe to top of back. A small patch of orange-red pigment with a few scattered melanophores on top of head over brain and a similar color combination in front of eyes across snout onto upper jaw. Dorsal surface of center of upper jaw with a white spot. Iris of eye black surrounded by a narrow white ring, remainder of iris orange-red. A few larger scattered melanophores on pectoral-fin base. All fins lacking color.

Distribution— Reported from the Great Barrier Reef, Western Australia, Northern Territory, Philippines, Okinawa, Palau, Guam, Hawaiian Islands, Seychelles, and Madagascar.

Remarks— Usually found on seawhips of the genus *Juncella*, but also found on mooring lines. Male-female pairs often occur on a single seawhip; eggs are laid in an encircling band on the seawhip. Has been taken in Hawaiian waters from Ni`ihau, Kaua`i, and Kona, Hawai`i.

Material examined— Hawaiian Islands: Ni'ihau: BPBM 37292 (1); Kaua'i: BPBM 37904 (1), 10 paratypes listed above.

Bryaninops tigris Larson, 1985

(Fig. 54)

Bryaninops tigris Larson, 1985, The Beagle (Occ. Pap. N. Terr. Mus. Arts Sci.) 2(1):70, Figs. 7–8. On dropoff halfway between Bird and South Islands, Lizard I., Great Barrier Reef. Holotype: AMS I.20730-017. Paratypes: BPBM 18073(6), other paratypes at various museums.

Diagnosis.— From Larson (1985). Dorsal-fin elements VI-I,7-8. Anal-fin elements I,8-9. Pectoral-fin rays 12–14 (usually 13), the lower three or four rays unbranched and thickened. Longitudinal scale series 32–59 (mean 47), the scales usually reaching to above pectoral-fin base, occasionally a little anterior to it. Midline of nape usually naked (rarely a few predorsal scales), abdomen naked midventrally, and usually the sides as well. Body slender, the depth at anal-fin origin 6.9–8.6 in standard length. Head width about equal to head depth. Snout length about equal to orbit diameter.

Figure 54. *Bryaninops tigris*, 30 mm TL, on black coral, Wetar, Indonesia.

Caudal fin truncate. Interorbital narrower than pupil diameter. Gill opening short, ending at or slightly anterior to lower edge of pectoral-fin base. Pelvic fins short and cup-like. Reported to 55 mm TL.

Color in alcohol.— Background color light cream. Sides of body lacking pigment. A slight concentration of brownish pigment immediately anterior to first dorsal-fin spine, and between spines three and four, and at base of spine six. Brownish spots also present along base of second dorsal fin between rays one and two, three and four, and at bases of rays five, six and seven. Scattered melanophores present on top of caudal peduncle. There is a series of seven brownish spots spaced along the anal-fin base and ventral surface of caudal peduncle. Scattered melanophores present on top of head behind eyes. A brownish bar extending from front of eye forward onto upper jaw. Caudal-fin base dark brown with less intense pigment extending out to end of fin. First dorsal fin with scattered melanophores, more concentrated anteriorly and distally. Second dorsal fin and anal fin with scattered melanophores.

Color in life.— Lower side of body blackish to dusky red or orange. Back transparent except for six or seven narrow dusky orange or red bars that are continuous with color of lower side, and a series of small spots of the same color dorsally on the body, one in each space between the bars. A white line along top of vertebral column. A dusky orange or red stripe from front of snout through eye and across postorbital head. Two transverse dusky orange bands on occiput. A prominent black blotch at caudal-fin base.

Distribution.— Known from the Chagos Archipelago, Gulf of Thailand, Solomon Islands, Great Barrier Reef, Tahiti, and the Hawaiian Islands.

Remarks— Commensal on black coral (*Antipathes*). Reported from depths of 15–53 m. The only Hawaiian specimens were collected in 53 m off Kauai on *A. dichotoma*.

Material examined— Hawaiian Islands: Kaua'i: PBM 18073 (6) paratypes, specimens small and dried. Indonesia: BPBM 37376 (7).

Bryaninops yongei (Davis and Cohen, 1968)

(Figs. 29, 33, and 55)

Cottogobius yongei Davis and Cohen, 1969, Bull. Mar. Sci. 18(4):752, Figs. 1, 4–6. Darvel Bay, Borneo. Holotype: USNM 200402.

Diagnosis.— From Larson (1985). Dorsal-fin rays VI-I,7-10 (usually 8 or 9). Anal-fin rays I,8-9. Pectoral-fin rays 13–17 (usually 15–17, mode at 16). Posterior half of body covered with ctenoid scales, those above midline extending forward to first dorsal fin. Longitudinal scale series 26–58 (mean 40). Body depth at anal-fin origin 5.4–8.1 in standard length. Head width greater than head depth. Snout slightly longer than orbit diameter. Gill opening reaching ventrally to below pectoral-fin base. Pelvic disc usually cup-like and short, not reaching anus, the spines with fleshy lobes. Recorded to 40 mm TL.

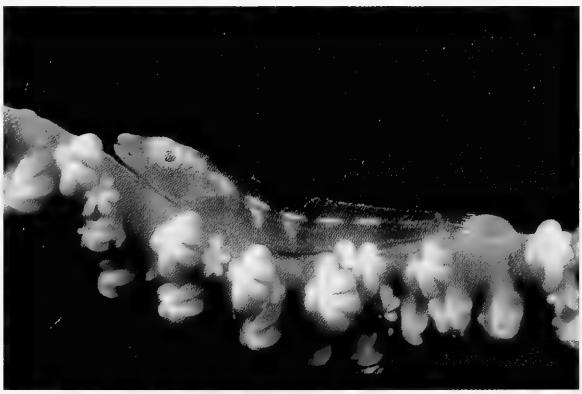

Figure 55. *Bryaninops yongei*, 35 mm TL, on seawhip, Molokini, Maui.

Color in alcohol.— Background color light cream. Body and fins lacking markings except for a few scattered melanophores on the pectoral-fin base, on the top of the head just behind the eyes, and immediately in front of the first and second dorsal fins.

Color in life— (from photograph of fish taken at Molokini, Maui in 27 m). Body translucent with backbone showing through as a silver stripe. Sides of body with a series of six dark brown triangular-shaped blotches, their apices pointing dorsally. Apex of first triangle located just anterior to first dorsal fin; second at end of first dorsal fin; third at second dorsal-fin origin; fourth at posterior third of second dorsal fin; fifth on caudal peduncle; and sixth at caudal-fin base. Coloration of head variable, one individual, with snout, mouth, cheeks and lower two-thirds of opercle dark brown to black and top of head white. Head of second fish translucent yellow with scattered melanophores on preorbital, snout, premaxilla and occiput. Pupil of eye black, surrounded by a narrow lemon yellow ring, remainder of iris orange-red, with a scattering of irregular black pigment on the outer perimeter. First dorsal-fin spines black, membranes clear. Rays of second dorsal, anal, caudal, and pelvic fins reddish, membranes clear. Pelvic-fin ray reddish and membranes clear except for white distal margin that rests on seawhip.

Distribution.— Red Sea to the Hawaiian Islands, Marquesas, Society Islands, and Rapa; Japan to Great Barrier Reef. Only Hawaiian specimens taken were three in 1967 (O'ahu, Lahilahi Point: USNM 203238; Moku Manu, O'ahu: BPBM 5571), two in 1968 (Hawai`i, Puakô: USNM 203237); and four in 2001 at Kâne'ohe Bay, O'ahu: CAS 218903.

Remarks.— Lives on the antipatharian seawhip *Cirrhipathes anguina* at depths of three to at least 45 m, typically with one male and female pair per seawhip, sometimes with a few juveniles as well.

Material examined.— Hawaiian Islands: Oahu: BPBM 5571 (1), Moku Manu; CAS 218903 (4), Kâne'ohe Bay. Seychelles: BPBM 35540 (2).

Cabillus caudimacula Greenfield and Randall, sp.nov.

(Figs. 40–41 and 56–57)

Material Examined.— Holotype: CAS 218110, male, 16 mm SL, Hawaiian Islands, O'ahu, Kâne'ohe Bay, sand field at seaward edge of spur and groove habitat outside of barrier reef, adjacent to rubble patch and pavement, (15.2–16.8 m), collected by R.C. Langston, 29 August 2002, field number L02-28. Paratypes: CAS 218111, 14.8 mm SL, USNM 375433, 16.8 mm SL, FMNH 113491, 14.8 mm SL, NTM S.15733-001, 13.3 mm SL, AMS I.42940-001, 14.3 mm SL, NSMT-P 67809, 14.2 mm SL, all taken with the holotype. BPBM 37261, 18 mm SL, Hawaiian Islands, O'ahu, Kâne'ohe Bay, Sampan Channel near buoy, spur and groove, 12–13.5 m, 30 August, 1991, D.W. Greenfield and G. Cockrell (field number G91-26). BPBM 39246, 16.5 mm SL, Hawaiian Islands, O'ahu, Kahe Point, sand and rubble, (14.5 m), R.R. Holcom, 18 November 1998. BPBM 22628 (3) (former UH 1708) 15.0–17.4 mm SL, Hawaiian Islands, O'ahu, off Waikiki reef, W.A. Gosline, V.E. Brock, J.E. Randall et al., December 1952.

Diagnosis.— A small (largest 18.0 mm SL), light colored goby with a depressed head (width 1.4–1.8 into head length and always wider than deep); a bilobed tongue; pelvic-fin frenum greatly reduced, flat and not raised and turned back (outer margins about one-third pelvic spine length, shorter in center and easily torn), and the pelvic spines not thickened; a terminal mouth; chin with a small, slightly curved mental frenum, and no barbels present on underside of head; tips of upper pectoral-fin rays not free; cheeks without prominent vertical fleshy flaps that bear papillae; dorsal-fin origin behind pectoral-fin base; no spines on preopercle; dorsal-fin spines thin and flexible; no dermal crest anterior to first dorsal fin; body scaled forward to pectoral fin; first gill slit open.

Dorsal-fin elements VI-I,8-9. Anal-fin elements I,8-9. Pectoral-fin rays 16–18. Longitudinal scale series 24–25. Branched caudal-fin rays 13–16, usually 15. Two to three gill rakers on lower arch. Large dark spot covering caudal-fin base and out onto basal portion of fin. Pelvic disc longer than wide, reaching anal-fin origin. Body covered with scales, extending forward to pectoral-fin base. Two large scales with enlarged cteni at top and bottom of caudal-fin base, extending over fin rays. Scales absent from base of first dorsal fin and from head. Gill membranes fused to isthmus, gill openings not extending forward of pectoral-fin base. Caudal fin rounded. Jaws extending posteriorly to anterior margin of pupil. Interorbital very narrow, less than one pupil diameter. Largest specimen 22.3 mm TL.

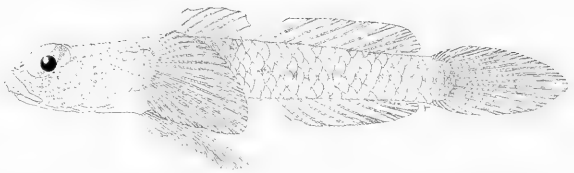

FIGURE 56. *Cabillus caudimacula*, out of BPBM 39246 (specimen lost); about 16 mm SL.

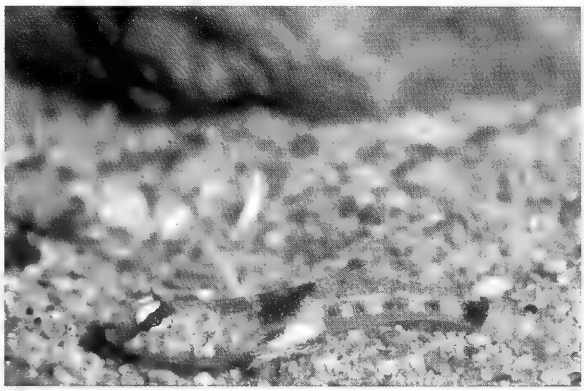

FIGURE 57. *Cabillus caudimacula*, paratype, BPBM 39246, 16.5 mm SL, Kahe Point, O'ahu.

DESCRIPTION.— Data for holotype presented first, followed by range for all specimens and mean or mode. Measurements as percentage of standard length. Data from 12 specimens, 13.3–17.9 mm SL. Dorsal-fin elements VI-I,9 (VI-I,8-9, usually I,9). Anal-fin elements I,8 (I,8-I,9, usually I,8). Pectoral-fin rays 17 (16–18, usually 17). Branched caudal-fin rays 15 (13–16, usually 15). Lateral scales 25 (24–25, usually 25). Gill rakers in four paratypes 1 + 2 (2), 1 + 3, 2 + 2. Head length 31.2 (30.3–34.7: 32.1). Head width 20.3 (17.3–24.1: 20.7). Head depth 13.7 (12.2–16.5: 14.4). Eye diameter 10.3 (9.2–11.5: 10.8). Snout length 6.2 (4.6–6.2: 5.6). Body depth 13.1 (12.6–18.9: 15.6). Caudal-peduncle depth 9.4 (9.3–10.9: 10.0). Caudal-peduncle length 21.6 (15.5–22.3: 19.3). First dorsal-fin base 15.6 (10.4–18.3: 13.9). Second dorsal-fin base 25.9 (21.3–28.5: 25.4). Anal-fin base 20.3 (16.9–23.3: 20.6). Caudal-fin length 26.6 (26.3–31.2: 27.9). Pectoral-fin length 25.6 (25.3–31.1: 28.2). Pelvic-fin length 23.1 (23.1–36.1: 29.3). Anterior nostrils tubular, extending anteriorly to upper lip. Posterior nostril with a low, raised ridge. A band of cardiform teeth present in both jaws, outer row the largest. Cheek with four rows of longitudinal sensory papillae: one directly under the eye, two in the center of the cheek, and the fourth at the bottom of the cheek. The following head pores are present: paired nasal pores, anterior interorbital, posterior interorbital, paired supraotics, paired anterior otics; intertemporal, a pore between the anterior otic and intertemporal, three preopercular pores.

COLOR IN ALCOHOL.— Background color of head and body white, with color pattern of black pigment. A distinctive dark blotch posteriorly on side of caudal peduncle and extending onto caudal-fin base. Four small blotches on midline of side of body, evenly spaced between front of second dorsal fin and blotch at caudal-fin base. A wide band running from ventral base of pectoral-fin axil posteriodorsally to first dorsal-fin base. Small blotches at base of second dorsal fin at elements three, five, eight, nine and 10, with scattered pigment extending onto dorsum to lateral midline from each blotch. A diffuse saddle on top of caudal peduncle joining blotch at caudal-fin base. A band running posteriorly from top of pectoral-fin base to join wide band under first dorsal fin; a

narrow extension from the band extending up to dorsal surface, crossing anterior to first dorsal fin, joining band on other side. Top of head and snout with scattered melanophores. An intense narrow black spot on midline of head midway between dorsal-fin origin and top of pectoral-fin base. A distinct bar running from anteroventral eye margin forward onto jaws. Cheek under eye and opercle with scattered melanophores. A cluster of melanophores on dorsal quarter of pectoral-fin base, extending out onto fin a short distance, remainder of fin lacks pigment as does the pelvic and anal fins. Caudal fin without pigment except for blotch at its base. Second dorsal fin with blotches at its base as previously described. First dorsal fin of one specimen with scattered blotches, the other almost completly black, an extension of the wide band running up from the body, with only the basal half of the first few spines lacking pigment. (Black pigment fades rapidly in preservation.)

Color in life.— (from photograph of live specimen from Kahe Point, O'ahu). Background color of head and body white. A distinctive black triangle on side of caudal peduncle and extending onto caudal-fin base, the apex of the triangle pointing anteriorly and the base extending onto the rays and membranes. A cluster of melanophores on body under pectoral fin. Three small, black spots on body midline spaced under second dorsal fin. A dusky blotch on top of nape and on top of head behind eyes. An oblique black band extending across eye and continuing onto upper and lower jaws. Pupil black, iris white. First dorsal fin clear except for a few black pigment spots at base of membrane behind last spine. Second dorsal fin clear except for small black spots on bases of elements three to five. Caudal, anal, pectoral and pelvic fins clear.

Etymology.— The specific epithet, *caudimacula*, is a compound adjective from the Latin *cauda* for tail and *macula* for spot, in reference to the prominent black blotch posteriorly on the body and caudal-fin base, the most distinctive color marking of the species.

Distribution.— Known at present only from O'ahu, Hawaiian Islands.

Comparison.— *Cabillus tongarevae* (Fowler, 1927) from Tongareva (an atoll also known as Penrhyn Id.) in the northern Cook Islands, the only other described species of the genus in the islands of Oceania, differs in having 13 branched caudal rays, 1 + 4 gill rakers, not having the two strongly ctenoid scales overlapping the base of the caudal fin, and in color; it lacks the large black spot below the dorsal fin and has prominent black spots on the dorsal fins (still visible on the holotype in the Bishop Museum). There is an excellent color photograph of *C. tongarevae* from the Ryukyu Islands in Masuda et al. (1984:274, pl. 354, fig. I). It is also positively known from Kanton Island in the Phoenix Islands (Schultz 1943), Marshall Islands (Randall and Randall 1987), and Great Barrier Reef, Australia (Russell, 1983). *Cabillus macrophthalmus* (Weber, 1909) was captured in Indonesia at a depth range of 120–400 m. The drawing (Fig. 31) in Koumans (1953), shows that it has a dark spot on the base of the front of the first dorsal fin, has a broad dark mark under the first dorsal fin that runs forward onto the nape, and lacks the large black spot at the caudal-fin base. *Cabillus lacertops* (Smith, 1959) has been reported from Mozambique, the Ryukyu Islands, and the east coast of northern Australia (Masuda et al. 1984), and Tonga (Randall et al. 2004). In the key to the species, Nakabo (2002) illustrated the coloration of *C. lacertops*, showing a distinct black mark at the caudal-fin base that turns upward. This species also lacks any black pigment on the body under the first dorsal fin. Hayashi and Shiratori (2003) also have photographs of *C. lacertops* and *C. tongarevae* (page 116).

Remarks.— Specimens were collected from sand near reefs at depths of 1.5–15 m.

Material examined.— *Cabillus tongarevae*: Marshall Islands, Enewetak Atoll: BPBM 10980 (1); Andaman Sea, Similan Islands (NW of Phuket): BPBM 22803 (1); Coral Sea, Chesterfield Bank: BPBM 33709 (1).

***Coryphopterus duospilus* (Hoese and Reader, 1985).**
(Figs. 38–39 and 58–59)

Fusigobius duospilus Hoese and Reader, 1985, J.L.B. Smith Inst. Ichthyol., Spec. Publ. No. 36:1-9. Escape Reef, Great Barrier Reef, Australia. Holotype: AMS I.22619-026.

Fusigobius neophytes africanus Smith, 1959, Ichthyol. Bull., Dept. Ichthyol., Rhodes Univ. No. 13:208, pl. 11F (in part, Aldabra and Pinda, Mozambique only).

Diagnosis.— Counts based on 27 individuals, 16.0–49.7 mm SL. Dorsal-fin elements VI-I,9. Anal-fin elements I,8. Pectoral-fin rays 18–19 (19). Longitudinal scale series 24–25. Pelvic fins united to form a sucking disc that is longer than wide, reaching to anal-fin origin. Frenum weak and easily torn. Interorbital very narrow, less than ½ pupil diameter. Scales on body ctenoid, becoming cycloid anterior to paired fins. No scales on operculum and no median predorsal scales. Jaws extending posteriorly to between anterior eye margin and pupil. Gill opening extending forward nearly to edge of preopercle. Head about as deep as wide, snout pointed. Body depth 4.3–5.8 in SL. Caudal fin rounded, slightly shorter than head. A small dark spot at center of caudal fin. First dorsal fin usually with dark markings on outer part, one on membrane between first and second spine, and second on membrane between second and third spine, angling to base of third spine. Largest specimen 57 mm TL.

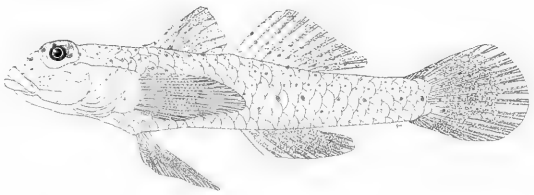

Figure 58. *Coryphopterus duospilus*, BPBM 19657, 45.2 mm SL.

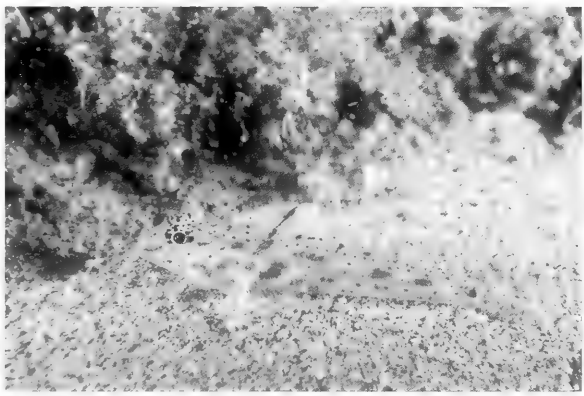

Figure 59. *Coryphopterus duospilus*, 32 mm TL, Kahe Point, O'ahu.

Color in alcohol.— Background color of head and body pale cream. Body with five irregular lines of light brown spots running length of body, upper two lines extending onto nape and head. A distinct dark brown spot on caudal-fin base, covering bases of five central fin rays. A light brown spot, filling most of the center of a scale, above and slightly posterior to dorsal surface of pectoral-fin base. A second more diffuse spot posteroventral to previous spot, located under pectoral fin. Top of head with series of small, light brown spots continuing forward from lines on body and a series of spots running forward from insertion of first dorsal fin onto nape, the one closest to dorsal fin the largest and most distinct. Side of head and snout with scattered small, dark brown spots. Eye with black pupil surrounded by silver iris, with small dark brown spots on upper two thirds, lower third under pupil lacking spots. Skin on top of eye with three dark brown lines running towards interorbital area. Pectoral-fin base with two light brown blotches, one on the upper third, the other on the lower third. Upper blotch narrowing and extending onto about four fin rays. A distinct dark brown bar on inside of fin at same location as bar on outside. Remainder of pectoral fin immaculate. Pelvic and anal fins clear. Caudal fin clear except for a few scattered light brown spots on membranes of basal half. First dorsal fin usually clear except for a dark brown spot at middle of second spine extending onto fin membranes anteriorly to first spine and posteriorly as

lighter spots across fin. Distinct dark brown spots at base of third spine and on body between spines five and six. First spine of second dorsal fin crossed by three evenly spaced dark brown bars. Remainder of fin with a few scattered light brown spots on membranes. Distinct dark brown spots at bases of rays two and six of second dorsal fin.

Color in life.— (from underwater photograph of fish taken at Kona in 18m) Background color of head and body translucent white. Five subcutaneous black blotches along backbone which has silver reflections: first under origin of first dorsal fin; second between first and second dorsal fins; third under posterior half of second dorsal fin; fourth behind second dorsal fin; fifth at caudal-fin base (blotches not visible in fresh specimens when clear tissue turns opaque white). About five irregular lines of small orange-brown spots running length of body, upper two lines extending onto nape and head. A series of silvery spots running along back at fin bases. Another row of silvery spots running along side from caudal-fin base to pectoral-fin axil about midway between midline of side and ventral body surface. Pectoral-fin base with two yellow-orange blotches, one on upper third, other on the lower third. Side of head with scattered yellow-orange spots of varying size. A row of small yellow-orange spots running anteriorly from anteroventral margin of eye across upper lip. Pupil of eye black, iris silver-yellow with a series of evenly spaced brown spots on upper two-thirds; lower third under pupil lacking brown spots. Pectoral, pelvic, and anal fins clear with silvery reflections. Caudal fin clear with scattered small silvery reflections and scattered orange-brown spots. Spinous dorsal fin clear on basal half, upper half with a yellowish tinge. A dark brown spot at middle of second spine extending onto fin membranes anteriorly and posteriorly. Second dorsal fin clear on basal half, upper half with a yellowish tinge, a few scattered orange-brown spots on membranes.

Distribution.— East coast of Africa to the Hawaiian Islands and Marquesas; Japan to Great Barrier Reef.

Remarks.— Typically found on sand and rubble next to reefs where it seeks shelter under coral or stones. Collected from 1–46 m. Hawaiian specimens of *Coryphopterus* were misidentified as *Fusigobius neophytes* (Günther) by Gosline and Brock (1960), a valid non-Hawaiian species. Randall (1995) placed *Fusigobius* in synonomy of *Coryphopterus,* a decision followed here; however, Thacker and Cole (2002) have argued that both genera are valid. The second, posterior, dark spot on the first dorsal fin appears to be less developed in specimens from the Hawaiian Islands than from other areas, but we were unable to find any morphological characters to separate the Hawaiian population.

Material examined.— Hawaiian Islands: O'ahu: CAS 218112(1), CAS 218113 (2), CAS 218114 (1), CAS 218115 (2), CAS 218116 (1), CAS 218117 (1), CAS 218118 (2), BPBM 19657 (3), BPBM 37262 (1), BPBM 37858 (1); Hawai'i: BPBM 15171 (1), BPBM 28733 (2); Maui: BPBM 28710 (5); Midway Atoll: BPBM 34769 (2). Ogasawara Islands: BPBM 35085 (2), BPBM 35159 (1), BPBM 35205 (3), BPBM 35237 (2). Marquesas: BPBM 12097 (1), BPBM 12766 (1). Palau: BPBM 19714 (1), BPBM 37722 (1). Maldives: BPBM 32978 (2).

Discordipinna griessingeri Hoese and Fourmanoir, 1978

(Fig. 60)

Discordipinna griessingeri Hoese and Fourmanoir, 1978, Japan. Jour. Ichthyol. 25(1):21, figs. 1–4. Holotype: USNM 214889. Paratypes: BPBM 5884 (1); BPBM 11266 (1).

Diagnosis.— Count for one Hawaiian specimen presented first, followed by counts from literature. Dorsal-fin elements V-I,8 (I,7-8, rarely 7). Anal-fin elements I,8. Pectoral-fin rays 18 (17–19). Longitudinal scale series 26 (22–25). Scales ctenoid posteriorly, cycloid anteriorly. Large

FIGURE 60. *Discordipinna griessingeri*, CAS 218119, 28 mm TL, Kâne'ohe Bay, O'ahu.

cycloid scales on top of head, no scales on cheek or opercle. Body depth 5.2–5.8 in standard length. Head distinctly broader than deep. Origin of first dorsal fin far forward on body, above posterior end of opercle, and widely separated from the second dorsal fin. First two dorsal spines greatly prolonged in both sexes, the second longest, about 1.5 in standard length, extending well back above second dorsal fin. Pectoral fins large, about 2.3 in standard length, the rays with free tips. Pelvic sucking disc longer than wide, extending to anus. Caudal fin somewhat pointed, 2.5–3.0 in standard length. Jaws extending posteriorly to anterior margin of pupil. Interorbital narrower than pupil diameter. Gill openings extending forward to edge of preopercle. Reported to 29 mmTL.

COLOR IN ALCOHOL.— A broad dark brown stripe running from pectoral-fin base to caudal-fin base, covering most of lower half of body; body above midline cream with three narrow light brown stripes running posteriorly from above pectoral-fin base; ventralmost stripe joining dark brown stripe on lower body where cycloid scales end and ctenoid scales begin; middle stripe running back to caudal-fin base; dorsalmost stripe running back to top of caudal peduncle. Head cream with distinct dark brown spots on top, sides and ventral surface including spots on snout and upper and lower jaws. Pectoral-fin base with a median dark brown stripe extending out onto about half of fin, fin posterior to and below this stripe cream. Dorsal portion and remainder of fin dark brown. First part of dorsal fin uniform dark brown. Second part of dorsal fin with dark-brown stripe on lower one-third of fin; central third of fin cream with scattered melanophores on rays; distal third dark brown. Central rays of caudal fin cream, dorsal and ventral rays dark brown. Anal fin covered with scattered melanophores. Pelvic fins cream.

COLOR OF FRESH SPECIMEN.— (photograph of specimen from Kâne'ohe Bay-CAS 218119) Background color of head and body off-white. Upper half of body with three longitudinal light brown stripes running from above pectoral-fin base to caudal-fin base. Lower half of body from behind pectoral-fin base to caudal-fin base black. Sides and top of head covered with distinct black spots, a larger, oblong spot running from top of preopercle ventrally onto opercle. Pupil of eye black with a golden yellow rim, iris off-white with seven, evenly spaced, black spots. Pectoral-fin base black, extending out onto central rays and membranes of fin. Dorsal third of pectoral fin brick red, distal margin black with white edge. Portion of fin between black center and dorsal red part white; ventral portion below central black area white. Anal fin brick red with some dusky black except for white basal line and white distal margin. First spine of first dorsal fin white, remainder of fin brick red with overlay of black except for tips of spines which are white. Basal one-quarter of second dorsal fin black, next distal quarter white, remainder of fin brick red with two black ocelli, margin of fin white. Caudal fin with three distinct sections: dorsal third brick red with three black ocelli; central third white; ventral third brick red near white center grading into black ventrally, entire fin with narrow, white margin.

DISTRIBUTION.— Known from the Red Sea, St. Brandon's Shoals, Cocos-Keeling Islands, Papua New Guinea, Great Barrier Reef, Fiji, Tonga, Tahiti, Tuamotu Archipelago, Marquesas, Japan, and the Hawaiian Islands.

Remarks.— Collected from depths of 1–37 m. Cryptic in coral, known only from collections made with ichthyocide. The second author collected the first specimen of this species in 1967 in Tahiti from 27 m. The first Hawaiian specimen was collected by W. A. Gosline and his class at Kahe Point, O'ahu in 1968 with rotenone; the label states, "caught emerging from *Porites* near base." We both collected the second Hawaiian specimen in Kâne'ohe Bay, O'ahu in 3 m. The Tahitian specimen was brilliant red, and some others for which the life color is known have also been bright red. The drab red coloration of the Hawaiian specimen is in sharp contrast; it is not known if this is representative of the population in Hawai'i or if the shallow bay habitat influenced the color.

Material examined.— Hawaiian Islands: O'ahu: CAS 218119 (1).

Eviota epiphanes Jenkins, 1903

(Figs 4–6 and 61)

Eviota epiphanes Jenkins, 1903, Bull. U.S. Fish Comm. 22(1902):501. O'ahu , Hawaiian Islands. Holotype: USNM 50720; Paratypes: SU 8707 (6).

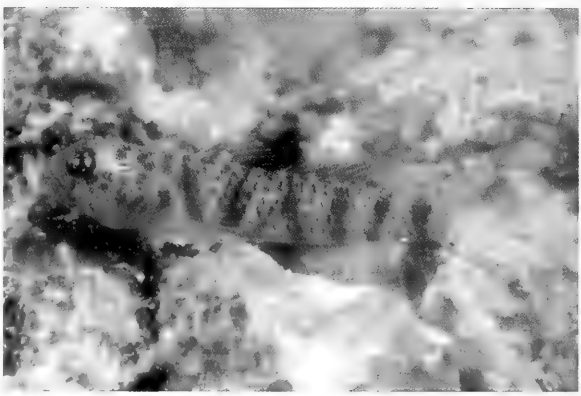

Figure 61. *Eviota epiphanes*, 17 mm TL, Kâne'ohe Bay, O'ahu.

Diagnosis.— Counts based on 20 individuals 12.3–14.7 mm SL. Dorsal-fin elements VI-I,8-VI-I,9 (VI-I,9). Anal-fin elements I,7-I,8 (I,8). Pectoral-fin rays 15–17 (17). Longitudinal scale series 23–24 (23). Pelvic fins separate with many side branches and finger-like; small, unbranched fifth pelvic-fin ray absent. Anterormost branch of fourth pelvic-fin ray short, with fewer than 10 segments; Genital papillae not ruggose. IT pore present. Spines in first dorsal fin not prolonged as filaments. A dark midpeduncular subcutaneous spot present towards midbase of caudal fin. Pectoral-fin rays 10–16 may be branched. Body covered with scales, extending anteriorly to a line between top of pectoral-fin base and origin of first dorsal fin. No scales on head. Caudal fin rounded. Interorbital very narrow, less than ½ pupil diameter. Jaws extending posteriorly about to posterior margin of pupil. Gill opening extending forward to a point midway between posterior margin of opercle and preopercle edge. Greatest body depth 4.0–5.3 in SL. Largest specimen 20 mm TL.

Color in alcohol.— Background color of head and body cream. Body with six faint subcutaneous bars, often only the most posterior one on caudal peduncle obvious. Base of scales pigmented with a line of several small brown spots, often more obvious on dorsal half of body. Four bars made up of small brown spots crossing head and nape. Anteriormost bar extending ventrally onto cheek. Area behind eyes anterior to first bar densely packed with small black spots. A distinct bar from ventral eye margin extending ventrally across cheek. Mouth and snout cream with few or no spots. Eye with black iris, pupil clear. Pectoral-fin base with scattered small brown spots on upper half, remainder of fin immaculate. Caudal and pelvic fins immaculate. First dorsal fin darker than second, pigment variable, almost solid black in some, to pigment only present on membranes between a few spines. Second dorsal fin with scattered pigment along base. Anal fin variable, from immaculate to a few scattered pigment spots.

Color of fresh specimen.— (taken from underwater photograph at Kâne'ohe Bay) Background color of head and body off-white. All markings on head and body composed of small black spots enclosed in a larger orange-brown area defining a spot or bar. Base of scales on body pigmented as above, forming rows of chevrons along sides. Head and nape crossed by four rows of blotches forming bars, the anterior one extending ventrally onto cheek. Cheeks with small spots and a distinct bar from ventral eye margin down across cheek. Snout and jaws orange-brown. Pectoral-fin base with blotch on upper half, fin immaculate. First dorsal fin orange-brown along base and darker distally, membranes before and after sixth spine black. Second dorsal fin lighter than first, with several orange-brown blotches along base. Pelvic and anal fins immaculate. Caudal fin with red on rays and membranes. A series of six subcutaneous bars on body: first anterior to first dorsal spine, second under first dorsal fin, third at second dorsal fin origin, fourth at center of second dorsal fin, fifth just posterior to second dorsal fin, and sixth on caudal peduncle just anterior to caudal fin. Iris and pupil of eye black.

Distribution.— Hawaiian Islands, Johnston Island, Line Islands, Ogasawara Islands, and southern Japan.

Remarks.— In a survey of the fishes of Kâne'ohe Bay, O'ahu, this was the most abundant species taken (Greenfield 2003). Boehlert and Munday (1996) reported that species in the genus Eviota composed the most abundant taxon in their ichthyoplankton samples taken near O'ahu. Because of their small size, these gobies are seldom seen by divers, but because of their numbers they must play an important role in reef ecology.

Material examined.— Hawaiian Islands: O'ahu: CAS 218096 (276), BPBM 38391 (33).

Eviota rubra Greenfield and Randall, 1999

(Figs 8–9 and 62)

Eviota rubra Greenfield and Randall, 1999, Copeia 1999: 439–446. Kâne'ohe Bay, O'ahu, Hawaiian Islands. Holotype: BPBM 38385. Paratypes: BPBM 35422 (3), BPBM 35424 (11), BPBM 37257 (3), BPBM 38386 (3), BPBM 38387 (14).

Diagnosis.— Counts based on 16 individuals 10.4–14.9 mm SL. Dorsal-fin elements VI-I,8-VI-I,9 (VI-I,8). Anal-fin elements I,7-I,9 (I,8). Pectoral-fin rays 15-17 (16). Longitudinal scale series 22–25 (25). Pelvic fins separate with many side branches and fringe-like; small unbranched fifth pelvic-fin ray present, about one-tenth length of fourth ray (often poorly ossified and difficult to see). Anterormost branch of fourth pelvic-fin ray elongate, with nine or more segments. Genital papillae of male and female ruggose. IT pore absent, POP pore present. No dark ventral-midline spots or midpeduncular subcutaneous spot towards midbase of caudal fin. Spines in first dorsal fin not prolonged as filaments. Pectoral-fin rays 9–16, may be branched. Body covered with scales, extending anteriorly to a line between top of pectoral-fin base and origin of first dorsal fin. No scales on head. Caudal fin rounded. Greatest body depth 4.1–5.6 in SL. Interorbital very narrow, less than ½ pupil

Figure 62. *Eviota rubra*, 15 mm TL, off Kâne'ohe Bay, O'ahu, 25 m.

diameter. Jaws extending posteriorly about to posterior margin of pupil. Gill opening extending forward to a point midway between posterior margin of opercle and preopercle edge. Largest specimen 19 mm TL.

Color in alcohol.— Background color of body and head light cream, without pigment. Subcutaneous bars absent in specimens from deeper water, but specimens from shallower stations (12–15 m) with faint subcutaneous bars. Head with a few, scattered, tiny red-brown pigment spots. Elements and membranes of first and second dorsal, anal and caudal fins covered with small, distinct reddish brown spots. No pigment on pectoral or pelvic fins.

Color of live and fresh specimens.— Body translucent with bright red markings when alive, but translucent areas turn white at death. Two distinct color forms, male with lemon-yellow on head and a second (females and perhaps immature males) without yellow. Following description of female color is from a live specimen photographed by R.R. Holcom at Pûpûkea, O'ahu: Body translucent, backbone, neurocranium and body cavity showing through as white with silver reflections. Silver reflections also scattered along dorsal and ventral margins of body, most likely ends of neural and haemal spines. Series of nine red, subcutaneous bars extending from dorsal to ventral side of body overlying silver backbone and body cavity. First bar above pectoral-fin base; second at center of first dorsal fin; third between spines five and six of dorsal fin; fourth at rays two-six of second dorsal fin; fifth at rays eight and nine; sixth at last two rays of second dorsal fin; seventh, eight and ninth on caudal peduncle. Additional red pigment on surface of body at locations of subcutaneous bars and also joining bars at midline to form H-like patterns. Pectoral-fin base red, with a silver stripe running dorsoventrally across base separating red into upper and lower portions. Nape to top of head crossed by four red bars. Upper and lower jaws and snout red. Upper half of operculum red, lower half and remainder of cheek translucent except for a narrow red bar from ventral margin of eye down to lower surface of head. Pupil of eye black, iris silver with blotches of bright red. Pectoral-fin rays pinkish, membranes without pigment. Pelvic fins lack pigment. Fin elements of first and second dorsal, anal and caudal fins with alternating red and pink bands, membranes with heavy scattering of tiny reddish brown pigment spots.

Color of male taken from slide of specimen photographed underwater at Kâne'ohe Bay shortly after capture. Color pattern on body as in female except that transluscent areas now are white due to death. Subcutaneous color pattern still partially visible. Cheek, snout, underside of head and gill membranes bright lemon-yellow. A wash of red over the yellow upper and lower jaws. Bar under eye red. Top of head with scattered larger melanophores. Fin color as in female except that distal two-thirds of both dorsal fins and anal fin with heavy peppering of black pigment. Basal third of second dorsal and anal fins yellow.

Distribution.— Hawaiian Islands.

Remarks.— Of the three species of *Eviota* known from Hawaiian waters, this is the deepest dwelling, usually being taken at ledge and deep spur and groove habitats (12.2–28.7 m) at Kâne'ohe Bay, and was the only *Eviota* species taken at depths greater than 18.3 m (Greenfield, 2003). The species typically is red, hence the name *rubra*, and can be separated from *E. epiphanes*, with which it coexists in the deep spur and groove habitat, because it lacks the black midpeduncular subcutaneous spot toward the midbase of the caudal fin that is present in *E. epiphanies*.

Eviota susanae Greenfield and Randall, 1999

(Figs. 10–12 and 63)

Eviota susanae Greenfield and Randall, 1999, Copeia 1999:439–442. O'ahu, Hawaiian Islands. Holotype: BPBM 38379. Paratypes: BPBM 38380 (1), BPBM 38381 (7), BPBM 38382 (3),BPBM 38383 (2).

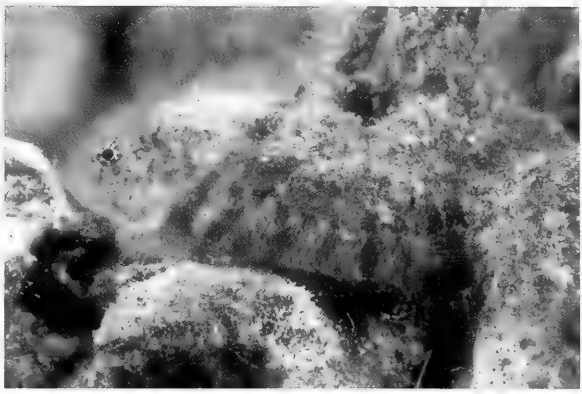

FIGURE 63. *Eviota susanae*, 19 mm TL, off Kâne'ohe Bay, O'ahu, 1 m.

DIAGNOSIS.— Counts based on 12 individuals 14.7–19.8 mm SL. Dorsal-fin elements VI-I,8-VI-I,9 (VI-I,8). Anal-fin elements I,6–I,8 (I,8). Pectoral-fin rays 15–18 (16). Longitudinal scale series 24–26 (25). Pelvic fins separate with many side branches and finger-like; small, unbranched fifth pelvic-fin ray present, about one-tenth length of fourth ray (often poorly ossified and difficult to see). Anterormost branch of fourth pelvic-fin ray elongate, with 10 or more segments. Genital papillae of male and female ruggose. IT pores absent and POP pores absent or greatly reduced. Spines in first dorsal fin not prolonged as filaments. Four to six (usually six) large dark spots on ventral midline posteriorly from anal-fin origin; subcutaneous bars associated with some ventral-midline spots. No dark midpeduncular subcutaneous spot towards midbase of caudal fin. Pectoral-fin rays 9–17, may be branched. Body covered with scales, extending anteriorly to a line between top of pectoral-fin base and origin of first dorsal fin. No scales on head. Interorbital narrow, less than ½ pupil diameter. Caudal fin rounded. Greatest body depth 4.2–6.8 in SL. Jaws extending posteriorly about to posterior margin of pupil. Gill opening extending forward to a point midway between posterior margin of opercle and preopercle edge. Largest specimen 25 mm TL.

COLOR IN ALCOHOL.— Background color of head and body cream. Scale pockets from origin of first dorsal fin back to caudal-fin base with crescents of dark brown pigment. A narrow dark brown line running along middle of body. Four-six (usually six) dark brown spots on ventral surface of body from anal-fin origin to caudal-fin base. An additional, smaller, less intense spot may be present near insertion of ventral procurrent caudal-fin elements. Corresponding dark brown spots on dorsal surface of body. Some of these external spots are at ends of subcutaneous bars (more obvious in fresh specimens) extending from dorsal to ventral surface of trunk. Pectoral-fin base peppered with melanophores, often concentrated into darker upper and lower blotches. Four dark brown bars crossing back anterior to first dorsal fin and top of head, either distinct or indistinct. Ventral side of body with scattered melanophores. Side of head mottled in females with indications of a bar from anterior ventral margin of eye down across cheek; in males the bar is narrower and there is less pigment on cheek. Upper and lower jaws with scattered melanophores, pigment under chin. Pectoral fins with light scattering of melanophores on membranes. Pelvic fins lack pigment. Caudal fin with bar across base where scales are present, remainder of fin with heavy peppering of melanophores. Anal and second dorsal fins with heavy peppering of melanophores. First dorsal fin with heavy peppering of melanophores and black spot on membrane posterior to last spine.

COLOR OF FRESH SPECIMEN.— (from photograph of specimen taken at Kâne'ohe Bay, male) Lower side of head lemon yellow, including below eye, all of upper and lower jaw, snout onto interorbital, lower half of cheek and opercle, all of gill membranes, and under lower jaw. Markings on head rust-orange over yellow, a distinct bar from ventral margin of eye down across cheek. Pupil of eye black, iris golden-silver with blotches of reddish brown. Top half of head and rest of body white with rust orange markings. Pectoral-fin base rust orange overlaid with scattered melanophores except for a white bar on central portion angling anterodorsally up onto opercular

membrane. Base of scales on body with rust orange pigment. Genital papilla white. Basal three-fourths of caudal fin peppered with mixed red and black pigment spots giving an overall reddish appearance, distal one-quarter white with fewer black pigment spots. Anal fin with similar mixture of red and black pigment spots, but more black than red; base of fifth ray with a red spot, tips of spine and rays white. First dorsal-fin spines with alternating red and white sections, membranes with same mix of red and black pigment as caudal and anal fins, but more black than in second dorsal-fin membranes; black spot on membrane behind sixth spine. Second dorsal fin with mixture of red and black spots as in anal fin, but more red than black, basal one-half more red, tips of rays white. Pectoral fins with red pigment on basal two-thirds of rays, scattered black and red spots on membranes of basal three-fourths, distal one-fourth clear, tips of rays white. Females-color same as males except no yellow on head which is white with more rust orange bars radiating out on cheek from eye.

Distribution.— Hawaiian Islands.

Remarks.— This is a species that typically is found in very sheltered areas, often part of the fouling community (Greenfield, 2003). In fact, the type locality of this species is the floating boat dock at the Hawaii Institute of Marine Biology in Kâne'ohe Bay. It is the largest of the *Eviota* species in the Hawaiian Islands, reaching a length of 18.5 mm SL.

Gnatholepis anjerensis (Bleeker, 1851)

(Figs. 34–36 and 64)

Gobius anjerensis Bleeker, 1851, Nat. Tijdschr. Ned. Indië 1:251, fig. 11. Java. Holotype unknown; Neotype BPBM 26651.

Gobius ophthalmotaenia Bleeker, 1854, Nat. Tijdschr. Ned. Indië 7:46 (type locality, New Selma, Cocos-Keeling Islands).

Gobius capistratus Peters, 1855. Monats. Akad. Wiss. Berlin 1855:443. (type locality, Ibo, Mozambique).

Gobius deltoides Seale, 1901, Occ. Pap. B.P. Bishop Mus. 1(3):125 (type locality, Guam).

Gnatholepis knighti Jordan and Evermann, 1903, Bull. U.S. Fish Comm. 22:204 (type locality, Hilo,Hawai'i); 1905:487, pl. 58.

Gnatholepis corlettei Herre, 1936, Zool. Ser., Field Mus. Nat. Hist. 21:356, fig. 20 (type locality, Bushman Bay, Malekula Island, Vanuatu).

Diagnosis.— Counts based on 25 individuals 30.0–47.8 m SL. Dorsal-fin elements VI-I,10-11 (I,11). Anal-fin elements I,11. Pectoral-fin rays 15–17 (70% 16, 13% 17). Longitudinal scale series 30; ctenoid scales on body extending anteriorly to below origin of spinous dorsal fin (sometimes forward on side of nape to above middle of opercle); predorsal scales extending to posterior interorbital space, cycloid scales ventrally on abdomen, on prepelvic and prepectoral areas, and on opercle and cheek (rarely a few ctenoid scales posteriorly on opercle of large specimens); usually a few small scales on cheek entirely anterior to dark bar below eye. Narrow (less than pupil diameter) subcutaneous black bar extending down from under eye across cheek and under head. Pelvic fins united to form

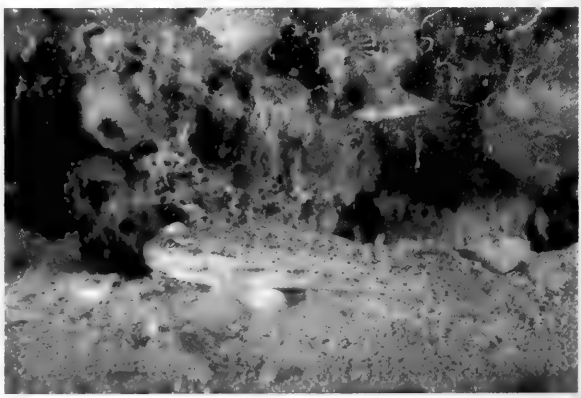

Figure 64. *Gnatholepis anjerensis*, 58 mm TL, Kâne'ohe Bay, O'ahu, 1.5 m.

a disk, longer than wide, almost reaching anal-fin origin; frenum broad. Gill membranes broadly united to isthmus, opening ending just below pectoral-fin base. Jaws extending posteriorly to between anterior margin of eye and pupil. Interorbital very narrow, less than one pupil diameter. Body depth 3.9–4.6 in SL Caudal fin rounded, usually slightly longer than head. Largest specimen 105 mm, but rarely exceeds 80 mm TL.

Color in alcohol.— Color varies greatly depending on the habitat, with individuals from sand areas being much lighter and those from dark habitats such as mangrove mud, much darker. Color descriptions of specimens from both habitats are given.

Sand habitat— Background color of head and body light cream. Head with a narrow, subcutaneous, dark brown to black bar running from ventral margin of eye, down across cheek to its ventral margin. Remainder of head covered with very small, scattered melanophores. A light brown blotch above pectoral fin, extending forward to eye as a line. Body with six elongate light-brown blotches along midline. A seventh blotch at caudal-fin base. Lighter bars entending up to dorsal surface from each blotch. Two of these blotches are at base of first part of dorsal fin, one on caudal peduncle and remainder at second part of dorsal fin. Scattered dark brown spots on blotches. Pectoral, pelvic and anal fins covered with small, dark brown chromatophores. First dorsal fin with a dark brown stripe running along basal one-third of fin, a narrow less pigmented stripe above this; remainder of fin dark brown. Second dorsal fin dark brown on membranes between rays that lack pigment. Caudal fin either without pigment or a few scattered dark brown spots.

Mangrove habitat— Background color of head and body medium cream. Subcutaneous dark bar under eye as in light form. A dark stripe running from posterior margin of eye posteriorly to above pectoral-fin base. A dark brown to black subcutaneous blotch running from margin of central portion of preoperculum onto operculum. Remainder of head covered with dense, small, dark brown spots, some coalesced into small blotches. Upper lip crossed by five dark brown bars, first at midline, one on each side midway between midline and end of premaxilla and another fainter bar at ends of premaxillas. Body blotches as in lighter color form except pigment darker and denser. Blotches at midline joined together resembling a stripe. A series of dark-brown spots arranged in rows running from pectoral-fin base back to caudal fin. Three rows above midline stripe and two below. Pectoral, pelvic, and anal fins as in lighter color form only darker. First dorsal fin as in lighter form except distal half of fin with an additional clear stripe in its center. Second dorsal fin with distinct dark spots arranged in five bars across fin. Caudal fin crossed by about eight rows of distinct spots.

Color in life.— (from color photograph taken of a 50-mm individual in shallow water on sand in Kâne'ohe Bay) Body white with silvery reflections on some scales. All markings referred to as "dark" are black-brown. A bright yellow humeral spot, the anterior half of yellow humeral spot surrounded by dark pigment that then runs forward to eye as a line. Pupil black, surrounded by a narrow yellow ring. Iris white, with a small dark spot at center at both the front and back of eye. A dark bar running from ventral edge of pupil down across cheek. A narrow, dark bar dorsally on eye, centered over posterior half of pupil. Snout with reticulated dark markings. Both upper and lower jaws with some dark markings. Opercle with a dark line extending from center of pectoral-fin base to edge of preopercle where it widens. Six dark blotches running along side of body, just ventral to midline. A series of much smaller, distinct, dark spots scattered along dorsal half of body anteriorly, and extending to lower half of body from second dorsal fin posteriorly to caudal-fin base. Pectoral and pelvic fins immaculate. Dorsal fins with a few, scattered small, dark spots. Caudal fin crossed by a number of rows of small, dark spots.

Distribution.— Red Sea and east coast of Africa to the Hawaiian Islands and islands of French Polynesia; southern Japan to Great Barrier Reef and Lord Howe Island.

Remarks.— *Gobius anjerensis* was described by Bleeker (1851) from a simple drawing without color markings of a specimen that had been collected in the period of 1821–1823 by Kuhl and van Hasselt from Anjer (now Anyer) in the Sunda Straight, Java. No specimen is extant. Bleeker (1874) selected *Gobius anjerensis* as the type species of the subgenus *Gnatholepis*, later elevated to a genus. Although one might guess that the drawing of *Gobius anjerensis* represents a species of *Gnatholepis*, it certainly cannot be identified to any known species. Were it not its selection as the type species of *Gnatholepis*, it would surely have been regarded as a *nomen dubium*. Randall and Greenfield (2001) have described a neotype of *Gnatholepis anjerensis* collected in the Java Sea off the southwest end of Sulawesi. It is one of the two most common species of the genus in Indonesia, and the species most often found in shallow water.

The Bishop Museum has 95 lots of *Gnatholepis anjerensis* ranging from the Red Sea and coast of East Africa to the Hawaiian Islands and Society Islands. Of the 62 lots for which there is information on the depth of capture, the specimens of 36 lots were collected from less than 2 m. Some were taken from tidepools, one from a brackish pool (salinity 12 o/oo). The deepest collection was from 46 m in the Red Sea; the deepest collection in the Hawaiian Islands was 26 m. Typically this species lives on sand very near coral reefs or rocky substrata into which it can seek shelter with the approach of danger. Of the 12 lots listed below that were collected around the island of O'ahu, seven were from Kane'ohe Bay.

Material examined.— Hawaiian Islands: Hawai'i: BPBM 28720 (1); Maui: BPBM 38359 (11) Moloka'i-BPBM 15132 (3); O'ahu: BPBM 1846 (1), BPBM 5495 (1), BPBM 7306 (5), BPBM 15040 (5), BPBM 15046 (13), BPBM 15130 (1), BPBM 15042 (21), BPBM 17800 (1), BPBM 19665 (10), BPBM 22649 (49), BPBM 31319 (1), BPBM 31320 (28), CAS 218120 (18), CAS 218121 (121), CAS 218122 (56); Kaua'i: BPBM 15041 (6); Midway Atoll: BPBM 34795 (1), BPBM 34873 (5). Johnston Island: BPBM 15043 (6), BPBM 15134 (3), BPBM 38361 (1).

Gnatholepis cauerensis hawaiiensis Randall and Greenfield, 2001

(Figs. 37 and 65)

Gnatholepis cauerensis hawaiiensis Randall and Greenfield, 2001, Ichthyol. Bull. J.L.B. Smith Inst. Ichth., no. 69:10, pl. II C, D. [Described as a subspecies of *Gnatholepis cauerensis* (Bleeker)].

Gobius cauerensis Bleeker, 1853. Nat. Tijdschr. Ned. Indië 4:269, (type locality, Cauer = Kauer, Sumatra).

Gnatholepis scapulostigma Herre, 1953, Philip. Jour. Sci. 82(2):193 (type locality, Enewetak Atoll, Marshall Islands).

Gnatholepis inconsequens Whitley, 1958, Proc. Roy. Zool. Soc. N.S.W. 1956–57:44 (type locality, Heron Island, Capricorn Group, Great Barrier Reef).

Acentrogobius cauerensis, Bleeker, 1983, Atlas Ichthyologique, unpublished plates for vols. XI–XIV. Smithsonian Inst. Press, Washington, D.C. Pl. 435b, fig. 1 (reproduction of previously unpublished color figure, without final corrections).

Diagnosis.— Counts based on 26 individuals 14.0–42.0 mm SL. Dorsal-fin elements VI-I,11. Anal-fin elements I,11. Pectoral-fin rays 16–18 (92% 17, 2% 16). Longitudinal scale series 30; ctenoid scales on body extending at least as forward as below origin of spinous dorsal fin, exceptionally on side of nape to above posterior margin of preopercle; predorsal scales extending to posterior interorbital space, cycloid scales ventrally on abdomen, on prepelvic and prepectoral areas, and on opercle and cheek (rarely a few ctenoid scales posteriorly on opercle); usually no scales on cheek entirely anterior to dark bar below eye. Narrow (less than pupil diameter) subcutaneous black bar extending down from under eye across cheek and under head. Pelvic fins united to form a disk, longer than wide, almost reaching anal-fin origin; frenum broad. Gill membranes broadly united to isthmus; gill opening ending slightly ventral to pectoral-fin base. Interorbital very narrow,

less than one pupil diameter. Body depth 4.2–5.1 in SL. Caudal fin rounded, usually slightly longer than head. Largest specimen, BPBM 15131, 56 mm TL, from Maui.

FIGURE 65. *Gnatholepis cauerensis hawaiiensis*, 50 mm TL, Kona, Hawai'i, 29 m.

COLOR IN ALCOHOL.— Body whitish to pale yellowish brown with a row of six large dusky blotches on lower side and brown longitudinal lines following center of scale rows (two rows darker when superimposed on dusky spots); a dark brown to black blotch above pectoral-fin base containing a small pale spot; a narrow blackish bar dorsally on eye from above center of pupil, crossing midinterorbital space; a prominent narrow black bar extending ventrally and slightly posteriorly from below middle of eye; dorsal fins with longitudinal rows of dusky dashes; large specimens developing dark lines, one per membrane, parallel to rays, in soft dorsal fin; caudal fin with a dark brown line in membranes between rays.

COLOR IN LIFE.— (from color photograph taken of 50-mm individual at 28.5 m on dark sand in Kona, Hawai'i) Body gray with six dark (brownish black) blotches running along side of body, just ventral to midline, with a large, blue area around and below each blotch. A cream to yellowish stripe running along midline just above blotches. A series of about six longitudinal lines along sides, running along center of scale rows. Lines dark brown in this specimen, but may be red or orangish-brown. Numerous small, blue spots along ventral half of sides, extending from caudal peduncle forward to front of eye. A bright yellow humeral spot present, surrounded by a black spot. A narrow, dark brown line running forward from humeral spot to eye, where it widens slightly. Iris of eye cream, pupil black, surrounded by a narrow golden ring. A prominent black bar starting at top of eye, across iris, through center of pupil, and continuing ventrally across cheek as the diagnostic feature for the genus. The bar across the cheek is as wide as the pupil (narrower in specimens living on a light-colored background). A dark brown line running from center of pectoral-fin base to preopercle where it widens. Snout and both jaws with reticulated black markings. Pectoral fins immaculate. Both dorsal fins gray with longitudinal rows of dark brown dashes. Caudal fin with reddish brown lines on membranes.

DISTRIBUTION.— Hawaiian Islands and Johnston Island.

REMARKS.— *Gnatholepis cauerensis* was first reported from the Hawaiian Islands by Randall and Greenfield (2001). It ranges from the coast of East Africa to the islands of Oceania; however, it has differentiated into at least four subspecies: wide-ranging from East Africa to the Society Islands; islands of the southeastern Pacific (Rarotonga, Austral Islands, Rapa, and Pitcairn Group), Easter Island, and the Hawaiian Islands. The Hawaiian population is distinct from the Indo-Pacific subspecies in having a slightly longer caudal peduncle (1.5–1.7 in head length, compared to 1.7–1.9), a dark line on membranes of the caudal fin instead of small dark spots, and numerous small blue spots on the lower side of the body. Also it rarely has small scales on the cheek entirely anteriorly to the dark eye bar.

The population at Johnston Island differs from the Hawaiian in having a slightly shorter caudal peduncle (1.6–1.8 in head) and by consistently having small scales on the cheek anterior to the dark eye bar. Knowledge of the life color is lacking.

Of the eight lots of *Gnatholepis cauerensis* taken in Hawaiian waters, one was obtained in 2 m, the others all from 14–29 m. As in *G. anjerensis*, this species is usually found on sand near the shelter of rock or reef.

Material examined.— Hawaiian Islands: Hawai'i: BPBM 28734 (1), BPBM 37860 (1), BPBM 37861 (3); Maui: BPBM 15131 (14); O'ahu: BPBM 7930 (1), BPBM 12284 (1) BPBM 37847 (1), BPBM 37859 (1); Midway Atoll: BPBM 15137 (1), BPBM 34770 (2).

***Kelloggella oligolepis* (Jenkins 1903)**
(Fig. 66)

Enypnias oligolepis Jenkins, 1903, Bull. U.S. Fish Comm. 22 (1902):504, Fig. 45. O'ahu, Hawaiian Islands. Holotype: USNM 50715.

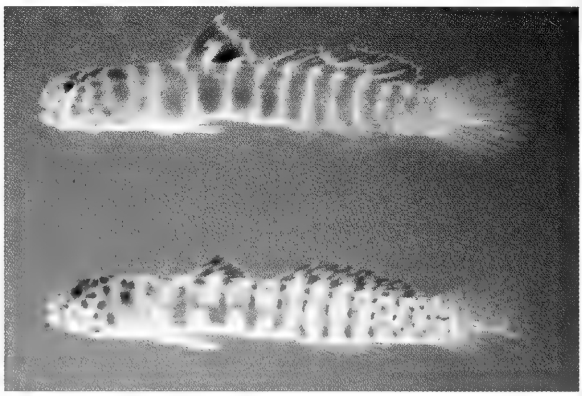

Figure 66. *Kelloggella oligolepis*, BPBM 39151, 17 mm SL, Barber's Point, O'ahu.

Diagnosis.— Counts based on 20 specimens 10.1–24.0 mm SL. Dorsal-fin elements VI-I,10-12 (I,11). Anal-fin elements I,6-8 (I,7). Pectoral-fin rays 12–13 (13). Body naked, with 10–11 dark vertical bars separated by narrow white bars. Snout rounded, its end either reaching upper jaw or slightly overhanging mouth. Gill membranes broadly united to isthmus. Jaws extending to under pupil. Interorbital narrow, about equal to pupil diameter. Pelvic sucking disc longer than wide, space between end of fin and anal-fin origin equal to or greater than pelvic-fin length; frenum broad. Greatest body depth 5.6–7.2 in SL. Caudal fin rounded. Maximum size 29 mm TL.

Color in alcohol.— *Mature male color pattern*: Background color cream. A distinct dark-brown spot on side of head above operculum, often joined by a light brown bar across top of head. An additional light brown bar across top of head anterior to first at preopercle. Diffuse dark brown spot at dorsoposterior margin of eye. Cheek variously marked with light brown bars reaching from posteroventral margin of eye and under chin. Body crossed by 10 light brown bars from anterior of first dorsal fin to caudal peduncle, eleventh bar on caudal peduncle present or absent: Bars separated by narrow white bars, narrow bars about ⅛ width of dark bars; first bar across back in advance of first dorsal fin extending to belly; second bar from front of first dorsal fin back to base of fourth spine and down to belly; third bar from bases of fifth to sixth spine down to lower part of side, lighter or absent on ventral surface; fourth bar from posterior end of first dorsal fin to origin of second dorsal fin, down to lower part of side, lighter or absent on ventral surface; sixth bar from posterior base of third dorsal-fin ray to base of sixth ray and down to anal fin; seventh bar extends from posterior of ray six to ray seven and down to anal fin; eighth bar from front of base of eighth ray to base of ninth ray and down to anal fin; ninth bar from bases of rays nine and ten down to ventral surface of caudal peduncle; tenth bar from base of last rays to behind end of fin down to ventral surface of caudal peduncle; eleventh bar, if present, encircling caudal peduncle. A diffuse spot at caudal-fin base. Ventral surface of body either cream or with a light scattering of melanophores. Pectoral, pelvic, anal, and caudal fins with scattered melanophores. First dorsal fin with scattered melanophores with distal half of fin darker in some specimens. Second dorsal fin with interspersed light and dark areas on membranes between every other fin element.

Immature and female color patterns (specimens 13.7 mm SL and less [immature]): Trunk of body without pigment, but about eight subcutaneous pigment bars visible through body. A series of 15 black spots on dorsal surface, two on top of head, two anterior to first dorsal fin, two along base of first dorsal fin, one between first and second dorsal fin, six along base of second dorsal fin and two on dorsal surface of caudal peduncle. Four black spots along anal-fin base and two on ventral surface of caudal peduncle. Distinct black spot on head above opercle. A series of black bars radiating out from behind and below eye. Pectoral, pelvic, anal, and caudal fins clear. Distal margin of first dorsal fin black and spots on body extending up onto fin. Second dorsal fin with black bars extending up onto fin from body spots. Specimen 17.8 mm (female): Body bars developing as external black spots along midline, dorsal surface, and adjacent to anal-fin base, at locations of subcutaneous pigment bars. A series of distinct black blotches on top, side and ventral surface of head. Pectoral, pelvic, anal, and caudal fins with some scattered melanophores and dark areas on dorsal fins more distinct.

Color of fresh specimens.— (from color photograph of BPBM 39151, captured from tidepools at Barber's Point, O'ahu) Mature male color pattern as in color in alcohol except that background color of body white, bars and spots on body and head a dusky black, and background color of head yellowish-cream. Light areas on fins are clear and dark areas are dusky black, except for spot on posterior portion of first dorsal fin that is intense black. Female color pattern as in color in alcohol except that background color of body is cream and that of head yellowish cream. Pigment spots on body, head and fins intense black.

Distribution.— Hawaiian Islands and Easter Island. Although previously recorded from the Ryukyu Island, Japan, the *Kelloggella* species there is *K. quindecimfasciata*.

Remarks.— This species occurs in tidepools high in the splash zone. It seems improbable that there would be sufficient gene flow between fishes found in splash zone tidepools at the Hawaiian Islands and Easter Island; however, Hoese (1975) examined specimens from both localities and was unable to find any differences except that the bands on the body are slightly narrower in Easter Island specimens. We also have examined specimens from Easter Island and the Hawaiian Islands, and also were unable to determine any differences other than the color character mentioned by Hoese. Three other fish species are known to have this unusual antitropical distribution, and a number of mollusks found at Easter Island are also only known from the Hawaiian Islands. One can postulate that these are species that were once more widespread when waters were cooler in the past, and now have been isolated to the north and south.

Material examined.— Hawaiian Islands: O'ahu: BPBM 5499 (14), BPBM 26370 (2), BPBM 31259 (1), BPBM 39151 (7), CAS 218123 (4). Easter Island: BPBM 6741 (2), BPBM 6742 (2).

Mugilogobius cavifrons (Weber, 1909)

(Figs. 22, 23, and 67)

Gobius cavifrons Weber, 1909, Notes Leyden Mus. 31 (note 4). Sula Takomi, Ternate, Moluccas, Indonesia. Syntypes: ZMA 112616 (43).

Diagnosis.— Counts based on 12 individuals 21.8–49.0 mm SL. Dorsal-fin elements V-I,7-VI-I,8 (VI-I,8). Anal-fin elements I,7-I,8 (I,8). Pectoral-fin rays 15–16 (16). Lateral scales 37–46 (39–40). Interorbital wide, greater than one eye diameter in individuals 37 mm SL or larger, and covered with very small cirri that extend onto snout and under eye on cheek. Pelvic sucking disc longer than wide, but short, space between posterior end of fin and anal-fin origin greater than pelvic-fin length; frenum broad. Body covered with scales, lateral scales anterior to second dorsal

fin smaller than those under second dorsal fin and on caudal peduncle. Scales extending onto top of head meeting cirri on interorbital and onto operculum. No scales on cheek. Caudal fin rounded. Depth of body about five in SL. Jaws extending to posterior margin of eye. Gill membranes broadly united to isthmus. Attains 58 mm TL.

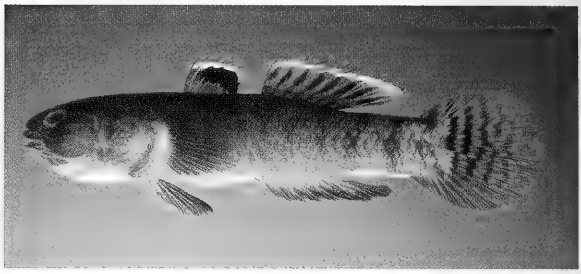

FIGURE 67. *Mugilogobius cavifrons*, BPBM 33492, 22 mm SL, Kâne'ohe Bay, O'ahu, 0.1 m.

COLOR IN ALCOHOL.— Background color dark cream, entire body and head overlaid by a heavy peppering of small, dark brown spots. A pattern of dark brown marks on upper half of body: the first a line angling posteroventrally from top of head above top of pectoral-fin base down to midline at line down from second dorsal-fin spine; a blotch between this line and front of first dorsal fin, sometimes blotch extends up to nape; second line from second dorsal-fin spine extending posteroventrally to body midline; third line from sixth dorsal-fin spine extending posteroventrally to body midline. Five bars on posterior half of body extending from dorsal surface to body midline: first at second element of second dorsal fin; second at fourth element; third at elements seven and eight; last two across caudal peduncle. A blotch at caudal-fin base. Two dark brown bars from posteroventral eye margin across cheek, upper bar reaching preopercular margin, lower bar midway to margin. Center of opercle near preopercular margin with a dark brown spot. Body patterns may be more diffuse in larger individuals. First dorsal fin with a dark brown stripe angling from front of fin down to base of last spine and following membrane; stripe beginning on upper third quarter of fin, with clear areas on lower half and upper quarter. Larger males may have scattered pigment on lower half of fin and black on distal fin margin. Second dorsal fin with dark brown pigment on lower three quarters being more concentrated on membranes midway up fin. Dark pigment on fin more extensive on larger males. Pectoral, pelvic, and anal fins densely covered with melanophores. Caudal fin crossed by four to five bars.

COLOR IN LIFE.— (from photograph of living specimen taken at Kâne'ohe Bay) Background color tan, color patterns overlaying tan are black. Head with a series of distinct lines: One from snout to anterodorsal portion of eye; another from middle of side of upper jaw to ventral margin of eye; a line from posteroventral eye margin to edge of preopercle; a long wavy line from end of jaws across ventral portion of cheek onto opercle. Opercle, preopercle and nape with scattered irregular marks. Side of body with a number of irregular, broken narrow bars. Ventral surface of body light tan. Pectoral, pelvic, and anal fins dusky. Caudal fin crossed by four irregular, black bars. First dorsal fin crossed by two black bars, the first on distal one-quarter of fin and second on second quarter up from base, expanded to cover basal one-half posteriorly. Second dorsal fin dusky with some darker areas.

DISTRIBUTION.— Known from Indonesia, Papua New Guinea, Philippines, Taiwan, Ryukyu Islands, Kosrae (Caroline Islands), Guam, and O'ahu, Hawaiian Islands.

REMARKS.— This species was most likely unintentionally introduced into Hawaiian waters perhaps via ballast water of a ship. It was first recorded from the mangroves at Coconut Island, Kaâne'ohe Bay, O'ahu by Randall et al. (1993) as *M. parvus*, which is a synonym of *M. cavifrons* (Larson, 2001). This species now is widespread on O'ahu, being most common in shallow mangrove, brackish and freshwater habitats.

MATERIAL EXAMINED.— HAWAIIAN ISLANDS: O'ahu: BPBM 32479 (1), BPBM 33492 (1), BPBM 33931 (4), BPBM 34569 (2), BPBM 34997 (5).

***Opua nephodes* E.K. Jordan, 1925**
(Fig. 68)

Opua nephodes E.K. Jordan, 1925, Proc. U.S. Nat'l. Mus. 66(2570):36, pl. 2, fig. 2. O'ahu, Hawaiian Islands. Holotype: USNM 87419.

FIGURE 68. *Opua nephodes*, 35 mm, Kâne'ohe Bay, O'ahu, 2m.

DIAGNOSIS.— Counts based on 11 individuals 20.5–33.3 mm SL. Dorsal-fin elements VI-I,9-VI-I,11 (VI-I,10). Anal-fin elements I,10-I,11 (I,10). Pectoral-fin rays 17–19 (19). Longitudinal scale series 27–29 (28). First spine in second dorsal fin stout and sharp-tipped, first spine of first dorsal fin also stouter than following spines. Body with a line of dash-like dark marks running along midline of side and four fainter lines above. Pelvic sucking disc longer than wide, almost reaching to genital papillae, frenum broad. Body covered with scales extending forward on top of head to eyes. No scales on opercle or cheek. Gill openings extending forward to below posterior margin of eye. Jaws extending posteriorly to between front of eye and pupil. Interorbital very narrow, less than one pupil diameter. Caudal fin rounded, shorter than head. Greatest body depth 4.8–5.6 in SL. Largest specimen 57 mm TL.

COLOR IN ALCOHOL.— Head and body light cream with light brown markings. A series of five dash-like dark marks running along midline of side, first under middle of first dorsal fin; second under first third of second dorsal fin; third under last third of second dorsal fin; fourth at center of caudal peduncle; fifth at caudal-fin base. Four stripes above midline dashes, lower two running from caudal peducle forward to above pectoral-fin base. Third stripe running from top of caudal peduncle forward onto head and top stripe from base of second dorsal fin onto head. Side of head with diffuse bar under eye that extends posteriorly across cheek and onto opercle. Pectoral-fin base with diffuse pigment on upper half, no pigment on pectoral-fin rays or membranes. Pelvics, anal, and both dorsal fins with scattered melanophores. Caudal fin crossed by three light, indistinct bars.

COLOR IN LIFE.— (from photograph of live fish taken at Kâne'ohe Bay) Background color of head and body white. Body with six dark brown, longitudinal lines composed of separate dashes running the body length. Ventralmost line begins behind pectoral-fin base and joins the line above below second dorsal-fin origin. The latter line continues to caudal-fin base and has five prominent, evenly spaced, dark brown blotches on it, the last blotch at caudal-fin base. Two dorsalmost lines extending posteriorly from top of head onto body. Entire body and head overlaid with iridescent white blotches. Ventral surface of head and body white. Sides and top of head with scattered dark brown blotches. Eye with black pupil surrounded by golden ring, iris dark brown. Dark brown blotch on upper portion of pectoral-fin base. First dorsal fin peppered with melanophores. Second dorsal fin also peppered with melanophores, but with dark brown blotches on basal third of some rays. Anal fin peppered with melanophores. Caudal fin crossed by three irregular rows of dark brown blotches. Pectoral and pelvic fins clear, overlaid with small, scattered, iridescent white spots.

DISTRIBUTION.— Hawaiian Islands.

REMARKS.— Specimens have been collected from depth of 1–11.5 m on silty sand and also mud bottom. This species is common on the mud bottom of Kâne'ohe Bay, where along with

Oxyurichthys lonchotus, it is a common food item of hammerhead shark pups. The Honolulu Laboratory of the National Marine Fisheries Service has recently collected this species using a shrimp trawl from deep water (138–169 m) north of Moloka'i. The deep water specimens appear to have larger eyes than those taken in shallow water. Jennifer K. Schultz (pers. commun., April, 2004) compared tissue samples preserved in 70% ethanol of deeper water and shallow specimens using mitochrondial DNA cytochrome b and concluded that they are the same species. More specimens are needed to confirm the apparent larger eye of this goby from deeper water. This species has incorrectly been placed in the genus *Hazeus*.

Material examined.— Hawaiian Islands: Oahu: CAS 218124 (3), CAS 218125 (16), BPBM 4838 (1), BPBM 14648 (6), BPBM 17820 (21), BPBM 22641 (5) cleared and stained, UH 1772 (9); Maui: BPBM 34920 (5); Moloka'i: 39132 (3).

Oxyurichthys heisei Pezold, 1998

(Fig. 69)

Oxyurichthys heisei Pezold, 1998, Copeia 1998(3):687–689. Holotype: BPBM 15473. Paratypes: BPBM 34513 (4), BPBM 24145 (3), BPBM 24151 (2), BPBM 24140 (1), BPBM 24084 (1), CAS 74809 (2), LIAIP 1968466 (1), LIAIP 1968467 (1), NLU 64915 (2).

Diagnosis.— Counts from Pezold (1998) based on type material (49.4–63.7 mm SL). Dorsal-fin elements VI-I,12. Anal-fin elements I,13. Pectoral-fin rays 21–23 (22–23). Longitudinal scale series 50–64. Caudal fin distinctly pointed, more than twice as long as wide. Well-developed fleshy crest on nape extending forward from first dorsal fin to preopercle. Pelvic sucking disc longer than wide, not reaching beyond anus; frenum broad. Body covered with small scales extending forward to above midopercle on nape, but with naked median. No scales on cheek and opercle. Gill membranes fused to isthmus at level of middle of opercle. Jaws extending posteriorly to below middle or posterior third of orbit diameter in females, to below posterior margin of orbit in males. Interorbital very narrow, less than one pupil diameter. Greatest body depth 5.5–7.0 in SL. Largest specimen 118 mm TL.

Figure 69. *Oxyurichthys heisei*, 54 mm SL, off NW Moloka'i, 124 m (specimen lost).

Color in alcohol.— From Pezold (1998): Figure 69. *Oxyurichthys heisei*, 54 mm SL, off NW Moloka'i, 124 m (specimen lost). "No spot on eye; no spots on gular fold beneath preopercle or anterior process of quadrate; anterior nares not darkly pigmented; body uniformly yellowish brown with faint pigment on cheek beneath posterior portion of orbit (in one specimen, five faint midlateral patches of melanophores are discernible with a microscope); D1 lightly pigmented, but with dark streak between first and second spines, variably indicated (weakly represented in holotype); D2 lightly pigmented; caudal fin with scattered melanophores, dusky distally and between lowermost rays; anal fin lightly pigmented basally and marginally, with clear zone between bands; pelvic fins with few melanophores on connecting membrane, dusky in patches but primarily concentrated between distal branches of rays and proximally; between rays 2/3 and 4/5 in some specimens; pectoral fins unpigmented."

Color in life.— Unknown.

Distribution.— All known specimens are from deep water (124–143 m) off the coast of Moloka'i, Hawaiian Islands.

Remarks.— This is one of only two deep-dwelling gobies known from Hawaiian waters.
Material examined.— Hawaiian Islands: Moloka'i: CAS 218155 (1).

***Oxyurichthys lonchotus* (Jenkins, 1903)**
(Figs. 13–15 and 70)

Gobionellus lonchotus Jenkins, 1903, Bull. U.S. Fish Comm. 22(1902):503, fig. 44. O'ahu, Hawaiian Islands. Holotype: USNM 50698.

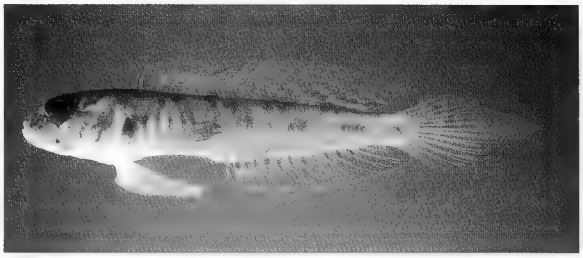

Figure 70. *Oxyurichthys lonchotus*, BPBM 37084, 47 mm SL, Kahana Bay, O'ahu, 0.1 m.

Diagnosis.— Counts based on 20 individuals, 28.7–39.1 mm SL. Dorsal-fin elements VI-I,12-VI-I,13 (VI-I,12). Anal-fin elements I,12-I,14 (I,13). Pectoral-fin rays 18–20 (19). Longitudinal scale series 77–88. Caudal fin pointed, more than twice as long as wide. Well-developed fleshy crest on nape extending forward from first dorsal fin at least past edge of opercle and farther in larger individuals. Body with a lateral series of elongate blotches. Dark spot on superior margin of eye. Prominent dark spot on pectoral-fin base and dark spots on branchiostegal membranes under lower jaw. Pelvic sucking disc longer than wide, almost reaching anal-fin origin; frenum broad with fringe on edge. Body covered with small scales extending forward on top of head to a line up from edge of preopercle. No scales on opercle or cheek. Gill membranes fused to isthmus at level of midopercle. Jaws extending posteriorly to mid pupil. Interorbital very narrow, less than one pupil diameter. Greatest body depth 5.3–5.7 in SL. Attains 130 mm TL.

Color in alcohol.— Background color of head and body cream. Sides of body with a series of light brown marks corresponding to dark gray marks in color description for fresh specimen. Top of head with a narrow dark brown line extending from posterior margin of one eye to the other eye; two faint, light brown bars crossing top of head posterior to this line. A dark brown blotch below posteroventral eye margin. A small dark brown spot on cheek above end of upper jaw. Anterior tubular nostrils black. Distal margin of crest on nape dark brown. Black spot on superior eye margin. Side of head with diffuse brown pigment on opercle. Isthmus with scattered brown chromatophores. Branchiostegal membranes under lower jaw with one or two dark brown blotches. Upper two-thirds of pectoral-fin base with a dark brown blotch. Pectoral, caudal, dorsal, and anal fins with scattered light brown chromatophores on rays and membranes. Pelvic-fin membranes dark brown, rays cream or with a few light brown chromatophores.

Color of fresh specimen.— (from photograph of specimen taken at Kahana Bay, O'ahu) Background color of body, top and sides of head grayish brown, ventral surface of head and body light gray. Body and head with small, scattered, iridescent blue spots. Sides of body with a series of dark gray marks, the first as seven narrow bands under the pectoral fin that almost reach dorsal and ventral surfaces. A dark blotch under end of pectoral fin. Four more blotches on side posterior to end of pectoral fin, the first under fourth element of second dorsal fin; second under seventh to ninth; third under 12th to 13th and past end of fin; and fourth on caudal-fin base. Another series of dark gray blotches along bases of both dorsal fins: first at first dorsal spine; second at third spine; third at fifth; fourth anterior to first spine of second dorsal fin; fifth at second element of second dorsal fin; sixth between elements five and six; seventh between elements six and seven; eighth

between elements ten and 11; and ninth at base of 12th element. Top of head with a black bar extending from posterior margin of one eye to the other; two blotches between this bar and first dorsal-fin origin. Side of head with a narrow dark gray bar running across center of opercle at a slight posterodorsal angle. A second lighter bar on preopercle paralleling opercular bar. A distinct, small, round, black spot on cheek above end of upper jaw. Dusky area between anteroventral margin of eye and upper jaw, black pigment on both nostrils. Eye with black pupil and orange iris, a black triangular-shaped mark on posteroventral margin of eye, narrow portion of triangle pointing anteriorly. Pelvic fins dusky. Pectoral fins with dark gray blotch on upper two-thirds of base, rays and membranes dusky. First dorsal fin with a dusky stripe on basal one-quarter, a white stripe distal to that on next one-quarter, and a narrow white stripe distal to the dark stripe. Ends of spines with an orange tinge. Second dorsal fin crossed by seven dusky stripes alternating with white stripes angling dorsoventrally across fin. Margin of fin with an orange tinge. Dorsalmost leading caudal-fin ray with alternating black and white bars, remainder of fin dusky, with darker pigment on posteroventral margin of fin and orange on margins in mature individuals. Anal-fin rays white basally with dusky blotches on membranes between rays on basal third of fin. Remainder of anal fin dusky with a white distal margin.

Distribution.— Hawaiian Islands.

Remarks.— This species is common in areas with soft mud bottoms such as that found around mangroves and at the bottom of Kane'ohe Bay, O'ahu. A series of collections using a small seine were made at Kahana Bay, O'ahu, and snapping shrimp (*Alpheus malabariacus*) were consistently taken along with the gobies. It is possible that *O. lonchotus* uses shrimp burrows for shelter.

Material examined.— Hawaiian Islands: O'ahu: CAS 218126 (26), CAS 218139 (115); BPBM 1884(1), BPBM 1885 (1), BPBM 1886 (1), BPBM 4884 (2), BPBM 5520 (1), BPBM 5521 (1), BPBM 15382 (13), BPBM 15386 (1), BPBM 37084 (2), BPBM 38854 (1).

***Pleurosicya larsonae* Greenfield and Randall, sp. nov.**
(Figs. 32, 71–72)

Material examined.— Holotype: CAS 218127, 11.4 mm SL, female, Hawaiian Islands, O'ahu, Kâne'ohe Bay, patch reef N. of Sampan channel, 1.2–3.1 m, 17 Nov. 2000, field no. G00-06, D.W. Greenfield, J.E. Randall, R.C. Langston, D.B. Eckert. Paratypes: CAS 218128 (6) 8.0–14.7 mm SL, taken with holotype. CAS 218129 (2) 12.9–15.9 mm SL, Hawaiian Islands, O'ahu, Kâne'ohe Bay, patch reef N. of Sampan Channel, 0–3.1 m, 8 Oct. 1992, field no. G92-03, D.W. Greenfield and N. Burke; BPBM 39152 (5) 12.1–13.5 mm SL, Hawaiian Islands, O'ahu, Kane'ohe Bay, patch reef NE of Crashboat channel, 0–3.1 m, 15 Apr. 1993, field no. G93-01, D.W. Greenfield; NTM S.15734-001 (3) 14.9–15.7 mm SL,same data as BPBM 39152; NTM S.15735-001 (2) 13.0–13.6 mm SL, Hawaiian Islands, O'ahu, Kâne'ohe Bay, patch reef N. of Sampan Channel, 2.4–3.1 m, 20 May 1993, D.W. Greenfield and K. Cole; USNM 375434 (1) 15.6 mm SL, Hawaiian Islands, O'ahu, Kâne'ohe Bay, patch reef at Crashboat Channel, 0–4.6 m, 4 May 1991, field no. G91-07, D.W. Greenfield, T. A. Greenfield, R.K. Johnson; FMNH 113492 (1) 14.7 mm SL, taken with holotype.; BPBM 39544 (1) 11.3 mm SL, Hawaiian Islands, O'ahu, Haleiwa, 6 m, 21 August 2004, R. R. Holcom.

Diagnosis.— Small *Pleurosicya* with a broad head and moderate snout, eyes set dorsolaterally. Second dorsal- and anal-fin rays I,7-I,8 (usually I,8). Pectoral-fin rays 17–18 (usually 17). Longitudinal scales 24. TRB 6. Nape naked. Pelvic fin rounded, cup-like, with fleshy, rounded pelvic spine lobes. Tongue round. Lower gill opening margin attached at level of preopercular mar-

gin. Gill membranes broadly joined to isthmus. Live color translucent with orange markings and some melanophores.

FIGURE 71. *Pleurosicya larsonae*, holotype, CAS 218127, 16.0 mm SL, Kâne'ohe Bay, O'ahu.

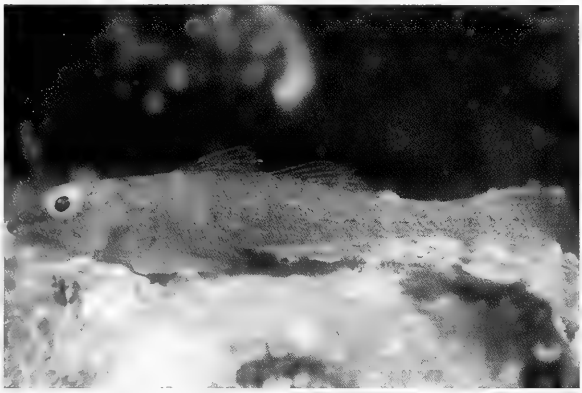

FIGURE 72. *Pleurosicya larsonae*, 15 mm TL, Kâne'ohe Bay, O'ahu, 2.5 m.

DESCRIPTION.— Description format follows Larson (1990) for ease of comparison. An asterisk indicates counts of the holotype. First dorsal-fin spines VI*. Second dorsal-fin elements I,7 (1), I,8(12)*. Anal-fin elements I,7(3), I,8(10)*. Pectoral-fin rays 17(8)*, 18(2). Lowermost pectoral-fin rays unbranched and thickened distally 4(3),5(7)*. Branched caudal-fin rays 10(7)*, 11(4). Scales ctenoid. Longitudinal scale count 23(1), 24(5)*,25(4). Nape naked. Gill rakers on outer face of first arch 2+1+6(1), 2+1+4(3) (holotype not counted). Gill rakers short. Lowermost half of lower limb of first gill arch bounded by membrane to opercle.

Measurements in percentage of SL based on 10 specimens 11.5–16.1 mm SL. Data for holotype presented first, followed by range and mean of all specimens. Head and anterior half of body roughly triangular in cross-section (apex dorsal) posterior half of body compressed. Body depth at anus 17.5 (13.2–17.5:15.3). Head length 34.1 (31.6–34.7:33.1). Head rather broad, width always greater than depth. Head width 19.2 (16.3–20.6:17.9.) [56 (48.2–60:54.3% of HL)]. Head depth 16.1 (14.7–17.2:15.9) [47 (42.3–51:47 % of HL)]. Snout moderate 10.9 (8.6–11.7:10.3) [32 (24.7–35:27.6% of HL)], rounded when viewed from above. Mouth subterminal, ending at point below anterior part of pupil of eye, 13.1 (13.1–17.5:14.8) [38 (38–54:44.7% of HL)]. Large upper lip overhanging mouth anteriorly, 3.9 (2.3–4.4:3.4) [11.5 (7–13:10.4% of HL)]. Lower lip very narrow. Eyes moderate 9.2 (7.9–11.2:9.5) [27 (24–35.3:28.8% of HL)]. Eyes set dorsolaterally, high on head. Interorbital space narrow, 2.2 (1.8–3.3:2.5) [6.4 (5.4–10:7.5% of HL)]. Anterior nostril in a short tube, posterior nostril in a larger tube, directly anterior to eye margin. Tongue rounded. Lower margin of gill opening attached at level of preopercular margin. Gill membranes broadly joined to isthmus at line between posterior eye margin and preopercular edge. Fins low, first dorsal shorter than anterior rays of second dorsal. Anal rays unbranched. Caudal fin rounded. Pectoral fins slightly pointed, reaching to gap between dorsals. Pelvic disc round, cup-like, just reaching anus. Frenum and pelvic spine lobes fleshy and fimbriate, lobes rounded.

Upper-jaw teeth very small, fine, and pointed; arranged in a band broader anteriorly, narrowing at sides. Four or five enlarged, slender, curved teeth present on each side of upper jaw spaced from front to side, mostly hidden by upper lip. Lower jaw with band of very small, fine, pointed teeth across front; band extending over edge of jaw, so that outermost enlarged and curved teeth angle outward. Sides of lower jaw with row of larger slightly posteriorly curved teeth; and one or two large curved canine teeth at each side of jaw symphysis. Lateral-line canals as for genus (Larson 1990: Fig. 5). Nape naked, scales on body extending anteriorly to area between top of pectoral-fin base and origin of first dorsal fin. Belly midline under pelvic fins naked. Male genital

papilla moderately long, flattened, with several tiny lobes at expanded tip. Female genital papilla short, cylindrical to slightly flattened, with several small lobes on either side of tip. Largest specimen 19.5 mm TL.

Color in alcohol.— Most color lost in alcohol, body straw yellow. A few scattered melanophores on top of head behind eye, cheek and on pectoral-fin base. A fine, short, dark line on middle of nape midway between eyes and first dorsal fin sometimes present (not in holotype). A few scattered melanophores sometimes present on body. Some dark markings as in Figure 71 retained on dorsal fins. Pigmentation shown in Figure 71 taken from underwater photograph showing fresh coloration.

Color of fresh specimen.— (from photograph taken underwater of freshly collected specimen at Kâne'ohe Bay) Head and body translucent with digestive tract and vertebrae clearly visible. Body overlaid with a pattern of orange markings as well as some melanophores. Head with a distinct orange band running anteriorly from front of eye to end of snout and across jaws, the most obvious color feature. An orange stripe running along length of lower jaw, and a fainter orange bar running up from end of maxilla to ventral eye margin. Scattered orange pigment extending along preopercular edge to eye. A narrow orange stripe extending from posterior eye margin posteriorly along midline, the stripe breaking up past pectoral-fin base into a series of about 10 dashes. Top of head with a distinct pattern of orange markings. A pair of stripes running from the anterodorsal eye margin towards the ascending process of the premaxilla as a V. Interorbital with two dashes centered along its length and a U-shaped marking at posterior portion of interorbital space with closed end posteriorly. A narrow orange stripe running anteriorly from dorsal-fin origin onto nape, splitting into a V that almost meets the U-shaped mark. Secondary stripes running from V to posterior eye margins. Nape directly posterior to eyes with scattered large melanophores. Pupil of eye black, iris silver-yellow with an orange ring around pupil. Digestive tract with distinct black spots showing through body. Spaces between vertebrae orange with orange pigment extending along neural and haemal spines. Body with some faint orange marbling. Pectoral-fin base with distinct large melanophores, base of pectoral-fin rays orange, remainder of fin clear. Pelvic disc clear, caudal fin clear with scattered orange spots. Anal fin clear with four orange spots with some scattered melanophores spaced along its base. First dorsal fin clear with an orange spot at the base of the first three spines, the fin crossed by three narrow black bars angling from the first spine posteriorly to fin base. Second dorsal fin clear, crossed by four orange bars with a few scattered melanophores at the base of last two fin rays.

Etymology.— Named in honor of Helen K. Larson of the Northern Territory Museum of Arts and Sciences, Darwin, Australia, whose revision of *Pleurosicya* laid the foundation for all future work on the genus.

Comparisons.— Separated from the following species with scaled napes because of its naked nape: *P. annandalei, P. australis, P. boldinghi, P. elongata, P. labiata, P. micheli, P. mossambica.* Separated from *P. prognatha* by lacking its distinctive elongate, pointed upper lip; from *P. spongicola* by lacking its very short, steep snout. From *P. plicata* by lacking its elongate pelvic-spine lobes and having a round rather than a trilobed tongue; from *P. bilobata* by lacking a distinct black blotch at rear of soft dorsal fin, lacking a bilobed tongue and differing in live coloration; from *P. fringilla* by lacking a black spot on anal fin anteriorly; from *P. carolinensis* by lacking large curved teeth at middle of each side of lower jaw and by having more pectoral-fin rays (17–18 versus 14–15, usually 15 in *P. carolinensis);* from *P. muscarum* by having the upper lip overhanging the lower jaw, versus a more terminal mouth in *P. muscarum,* by lacking the scattering of melanophores over body and five pairs of red lines radiating out from eye, and by having four to five lowermost unbranched pectoral-fin rays versus usually three or fewer in *P. muscarum.*

Pleurosicya larsonae is most similar to *P. occidentalis* and *P. coerulea.* It differs from *P. occidentalis* by lacking the intense elongate black spot on center of nape; however, like *P. coerulea,* it sometimes has a fine, short, dark line on the center of the nape. It differs from *P. coerulea* by having a narrower head (mean width 54.3% HL versus 72% in *P. coerulea),* shorter snout (mean length 27.6% HL versus 35% in *P. coerulea).* It also has a narrower upper lip, 7–13, mean 10.4% of HL versus 13.5, 13, and 12 in three paratypes (ANSP 165112) of *P. coerulea. Pleurosicya coerulea* is "translucent bluish to blue-green with two reddish stripes on head" (Larson, 1990:20), whereas *P. larsonae* is translucent gray with orange markings.

Distribution.— Known only from Kâne'ohe Bay, and Haleiwa, O'ahu, Hawaiian Islands.

Remarks.— This species is most certainly more widespread in the Hawaiian Islands but appears to be extremely cryptic. It was only collected five times in a total of 75 general ichthyocide collections, with four of those collections from a specific habitat, shallow patch reefs (0–4.6 m) with good circulation. Our sixth collection from that specific habitat only occurred after a number of futile attempts to collect more individuals for photographs. Members of the genus *Pleurosicya* generally are commensal with invertebrates or found on seagrasses and algae. Despite hours of searching we have never seen this species alive and thus do not know its specific association; however, Ronald R. Holcom (pers. commun., August, 2004) observed and caught a specimen at Haleiwa, O'ahu, that was living on *Porites compressa.*

Pleurosicya micheli Fourmanoir, 1971

(Figs. 28, 30, and 73)

Pleurosycia micheli Fourmanoir, 1971, Cah. ORSTOM Ser. Oceanogr. 9(4):499, fig. 8. Caban I., Philippines. Neotype: AMS I.21918-071.

Diagnosis.— Counts based on 10 individuals 14.0–17.1 mm SL. Dorsal-fin elements VI-I,8. Anal-fin elements I-8-I,9 (I,8). Pectoral-fin rays 16–18 (17). Longitudinal scale series 25–28 (27). Dark pigment on lower portion of caudal peduncle extending posteriorly as stripe onto caudal fin. Pelvic sucking disc longer than wide, almost reaching anus. Pelvic-fin frenum with thickened skin around pelvic spines that extend posteriorly over disc. Interorbital very narrow, about one-half pupil diameter, a single pore in center of interorbital space. Snout pointed from side view, jaws extending posteriorly to below about center of pupil. Body covered with scales, extending forward onto nape. No scales on opercle or cheek. Gill membranes free from isthmus, gill openings extending forward to posterior margin of pupil. Caudal fin rounded. Greatest body depth 5.0–7.1 in SL. Attains 25 mm TL.

Figure 73. *Pleurosicya micheli,* 25 mm TL, Kona, Hawai'i, 18m.

Color in alcohol.— Background color of head and body light cream. Scattered melanophores on lower half of body from anal-fin origin extending as a stripe onto lower half of caudal fin, becoming denser posteriorly. A line of melanophores running on dorsal surface of body along sides of both dorsal fins. A line of melanophores extending anteriorly from origin of first dorsal fin, extending anteriorly to cover area over brain. Scattered melanophores extending posteriorly from

posterior margin of eye onto top of preopercle. A few melanophores at top of pectoral-fin base. First dorsal fin clear except for a few large melanophores on lower half of membranes between spines four and six. Second dorsal, pectoral and pelvic fins clear. Anal fin with scattered melanophores between spine and first ray, remainder of fin clear. Lower three segmented rays of caudal fin clear, next four segmented rays dorsal to those densly pigmented dark brown, remaining rays of fin clear.

Color in life.— (from a photograph taken in 18 m at Kona, Hawai'i) Head and body translucent with internal coloration along backbone visible. A series of six dusky red blotches along backbone, with white areas on top of backbone between the blotches. A dusky red stripe running from end of backbone coloration onto lower middle part of caudal fin. A reddish area on side of head behind eye and a red to yellow stripe running from front of eye across snout to upper lip. Scattered black spots overlaid by red on top of head behind eyes. Eye with black pupil, iris silver with continuation of red stripes in front of and behind eye onto iris, top of iris with black edge. Fins clear except for a few scattered black spots on membranes of lower half of first dorsal fin.

Distribution.— Seychelles and Maldives to Hawaiian Islands and Society Islands; Ryukyu Islands and Taiwan to Great Barrier Reef, New Caledonia, and Loyalty Islands.

Remarks.— This species is commensal on a variety of hard corals, and appears to be the most common species of the genus over most of its range. It has been collected from depths of 15–38 m.

Material examined.— Hawaiian Islands: Hawai'i: BPBM 28736 (34).

***Priolepis aureoviridis* (Gosline, 1959)**
(Figs. 74–75)

Quisquilius aureoviridis Gosline, 1959, Pac. Sci. 13(1):68, fig. 1. O'ahu, Hawaiian Islands. Holotype: USNM 175013. Paratypes: BPBM 14203 [ex UH 1703] (8).

Diagnosis.— Counts based on 14 individuals 20.5–31.1 mm SL. Dorsal-fin elements VI-I, 11–VI-I,12 (VI-I,11). Anal-fin elements I,9–I,10 (I,9). Pectoral-fin rays 18–20 (19). Longitudinal scale series 28–30 (28). Predorsal scales 12–16. Body covered with scales, extending on top of head to eyes. No scales on opercle or cheek. Interorbital very narrow (less than ½ pupil diameter) but not forming a deep trench between eyes. Pelvic fin longer than wide, reaching past anus; frenum completely absent. Jaws extending posteriorly to anterior margin of pupil. Gill openings extending forward just past edge of preopercle. Greatest body depth 4.0–4.5 in SL. Caudal fin rounded. Largest specimen 47 mm TL.

Color in alcohol.— Background color of head and body cream overlaid with a peppering of scattered melano-phores that are more concentrated at scale margins. Body crossed by six faint brown bars extending from dorsal to ventral surface: first under fifth spine of first dorsal fin; second at origin of second dorsal fin; third at fifth element of second dorsal fin; fourth at tenth element; fifth about three scales past posterior end of second dorsal fin; sixth bar at caudal-fin base. Side of head with two faint light brown bars: first under center of pupil extending down across cheek; second from posterior eye margin across cheek to ventral margin of preopercle. Dorsal, anal, and caudal fins with scattered melanophores, no pigment on other fins.

Color of fresh adult specimen.— (from underwater photograph of freshly collected specimen at Kâne'ohe Bay) Background color of head and body lemon yellow. Head and body crossed by a series of narrow light gray bars. A bar under center of pupil extending down across cheek. Another bar extending from posterior eye margin down across cheek and also dorsally across top of head behind eyes. Three more bars between eyes across interorbital. Eye with black pupil, surrounded by a bright yellow ring, iris lemon yellow. Nape crossed by two bars, anteriormost at pos-

terior edge of preopercle, second one directly anterior to first dorsal fin. Six more bars on body, extending from dorsal to ventral surface: first under fifth spine of first dorsal fin; second at origin of second dorsal fin; third at fifth element of second dorsal fin; fourth at tenth element; fifth about three scales past posterior end of second dorsal fin; sixth bar at caudal-fin base. Scales on body with light brown margins. All fins lemon yellow with a peppering of melanophores on basal portions.

Color of fresh juvenile specimen.— Head and body lemon yellow with a heavy peppering of melanophores. Light gray bars as in adult. Second dorsal, anal, caudal, and pelvic fins lemon yellow with a heavy peppering of melanophores on membranes between yellow elements. Fin margins with a narrow band of black edged with white distally. First dorsal fin similar to other fins except for a black ocellus ringed with white on anteroventral portion of fin covering first five spines (Fig. 75). Pectoral fins lemon yellow with light peppering of melanophores.

Distribution.— Hawaiian Islands, Johnston Island, and Caroline Islands (Pohnpei and Ant Atoll).

Figure 74. *Priolepis aureoviridis*, 35 mm TL, Kona, Hawai'i, 20 m.

Figure 75. *Priolepis aureoviridis*, 25 mm TL, Kona, Hawai'i, 18 m.

Remarks.— This attractive, yellow species is found on outer reefs, but is not usually seen because it is secretive. In Kâne'ohe Bay it was most common at the deep spur and groove and ledge habitats (Greenfield 2003).

Material examined.— Hawaiian Islands: O'ahu: CAS 218901 (1), CAS 218902 (3), CAS 218899 (3), CAS 218170 (1), CAS 218169 (3), CAS 218168 (1), CAS 218132 (2), CAS 218898 (8), CAS 218900 (1), BPBM 7902 (6), BPBM 9860 (1), BPBM 12289 (4), BPBM 15461 (1), BPBM 24455 (1), BPBM 31017 (1), BPBM 34570 (1), BPBM 34571 (2), BPBM 34573 (1), BPBM 34535 (2), BPBM 35427 (5), BPBM 35778 (4), BPBM 37267 (4); Hawai'i: BPBM 10901 (2), BPBM 17825 (1), BPBM 17826 (1), BPBM 24799 (1), BPBM 28711 (1).

Priolepis eugenius (Jordan and Evermann, 1903)

(Figs. 44–45, and 76)

Quisquilius eugenius Jordan and Evermann, 1903, Bull. U.S. Fish Comm. 22(1902):203. O'ahu, Hawaiian islands. Holotype: USNM 50674 (missing). Paratypes: CAS-SU 7483 (3).
Gobiomorphus eugenius, Jordan and Evermann, 1905, Bull. U.S. Fish Comm. 23(pt. 1)(1903):357.

Diagnosis.— Counts based on 20 individuals 21.3–38.5 mm SL. Dorsal-fin elements VI-I,9-VI-I, 11 (VI-I,11). Anal-fin elements I,9. Pectoral-fin rays 18–20 (19). Longitudinal scale series

27–29 (27). Body covered with scales, extending anteriorly on top of head to eyes and ventrally on head to at least upper half of cheek and opercle. Interorbital very narrow (less than ½ pupil diameter), forming a deep trench between the eyes. Pelvic fin longer than wide reaching to anus, frenum completely absent. Jaws extending posteriorly to anterior margin of pupil. Gill openings extending forward to edge of preopercle. Caudal fin rounded. Greatest body depth 3.6–4.4 in SL. Largest specimen 54 mm TL.

FIGURE 76. *Priolepis eugenius*, 32 mm TL, Kâne'ohe Bay, O'ahu,1.5 m.

COLOR IN ALCOHOL.— Background color of head and body light brown. Body crossed by six dark brown, wide bars, positions as in fresh specimen described below. Pattern of dark brown bars on head as in fresh specimen. Eye with gray pupil, surrounded by black iris. First and second dorsal and caudal fins dark brown to black. Anal and pelvic fins dark brown to black with white margins. Pectoral fins light brown.

COLOR OF FRESH SPECIMEN.— (from underwater photograph of freshly collected specimen from Kâne'ohe Bay) Background color of head and body gray, overlaid with dark brown color pattern. Body crossed by six wide bars: first under first four spines of first dorsal fin; second from behind fifth spine to end of membrane of first dorsal fin; third under second to fourth elements of second dorsal fin; fourth under elements seven to nine; fifth behind last ray of fin onto caudal peduncle; sixth at center of caudal peduncle. Caudal-fin base with blotch. A wide bar crossing nape in front of dorsal fin and running down anterior to pectoral-fin base. Two narrow bars across head between posterior margin of eyes and bar on nape. Two narrow bars extending down from ventral eye margin across cheek, one from anteroventral margin of pupil and other from posteroventral pupil margin. Pupil black, surrounded by a red-orange ring, iris gray with bands dark brown radiating out from pupil. First and second dorsal fins, anal fin and pelvic fins black with a narrow white margin. Pectoral fins gray.

DISTRIBUTION.— Hawaiian Islands and Johnston Island.

REMARKS.— This species can be found in shallower water than the other species in the genus in Hawaiian waters. In Kâne'ohe Bay it was collected most often in the shallow spur and groove habitat, open patch reefs and even in tidepools, all areas with considerable water movement (Greenfield 2003).

MATERIAL EXAMINED.— HAWAIIAN ISLANDS: O'ahu, CAS 812130 (2), CAS 218166 (6), CAS 812131 (1), CAS 218167 (15), BPBM 8513 (1), BPBM 15349 (3), BPBM 19662 (6), BPBM 22626 (49), BPBM 22640 (4), BPBM 22671 (5), BPBM 37263 (2); Moloka'i, BPBM 4794 (2), BPBM 30225 (1); Midway Atoll, BPBM 34784 (2), BPBM 34799 (4), BPBM 34822 (1), BPBM 34855 (1), BPBM 34874 (6), BPBM 34891 (1), BPBM 35371 (1).

Priolepis farcimen (Jordan and Evermann, 1904)

(Figs. 43 and 77)

Gobiopterus farcimen Jordan and Evermann, 1904, Bull. U.S. Fish Comm. 22(1902):205. Hawai'i, Hawaiian Islands. Holotype: USNM 50654.

Zonogobius farcimen, Gosline and Brock, 1960, Handbook of Hawaiian fishes. University Press of Hawai'i, Honolulu, p. 270.

FIGURE 77. *Priolepis farcimen*, 16 mm, Kâne'ohe Bay, O'ahu, 1 m.

DIAGNOSIS.— Based on 7 individuals 10.1–15.5 mm SL. Dorsal-fin elements VI-I,8-VI-I,10 (VI-I,9). Anal-fin elements I,7-I,8 (almost always I,7). Pectoral-fin rays 17–18 (18). Longitudinal scale series 25–28 (26, often lost). Body covered with scales, extending anteriorly no farther than second spine of first dorsal fin. No scales on head or predorsal area. Interorbital narrow (about ½ pupil diameter). Pelvic fins longer than wide, reaching past anus, frenum completely absent. Jaws extending posteriorly to below middle of pupil. Gill openings extending forward just past edge of preopercle. Caudal fin rounded. Greatest body depth 3.6–4.4 in SL. Largest specimen 26 mm TL.

COLOR IN ALCOHOL.— Background color of head and body light cream. Body, head and fin membranes covered with a fine peppering of brown chromatophores. Color pattern on head (as described in color in life) fades easily in preservative but represented by faint brown lines. Distal margin of first dorsal fin dusky.

COLOR OF FRESH SPECIMEN.— (from underwater photograph of freshly collected specimen at Kâne'ohe Bay). Background color of head red-orange, overlaid by a series of distinct white lines edged in black: three lines crossing interorbital between eyes; a single line from anterior margin of eye running anteriorly to upper jaw; two lines extending ventrally from ventral margin of eye; a line crossing top of head posterior to eyes and continuing down across side of head to ventral surface, this line branching posteriorly to eye and extending as an additional line across top of head; a line crossing top of head at level of top of opercle, splitting above top of opercle, with one branch extending down along preopercular margin to ventral surface, the other branch extending down across pectoral-fin base. A short line crossing nape directly anterior to origin of first dorsal fin. Eye with black pupil, iris brunt orange. A series of about seven very short lines extending from bases of both dorsal fins ventrally to where distinct scale pattern begins. Background color of body gray (red-orange when alive) from pectoral-fin base back to origin of second dorsal fin where background color fades to a yellowish hue. Margins of scales with dark brown (black-orange when alive) edges forming a lattice pattern. Pectoral fin burnt orange at base grading into yellow distally. Spines of first dorsal fin with alternating clear and red-orange bands, membranes clear except for distal margin which is black. Second dorsal fin with alternating clear and burnt orange bands, membranes clear. Anal fin similar to second dorsal fin. Caudal fin with yellow tinge.

DISTRIBUTION.— Hawaiian Islands and Johnston Island.

REMARKS.— This is the smallest species of Priolepis in Hawaii, and can easily be separated from the other species in our area by the distinctive dark-bordered light lines that radiate out from the eye across the cheek and top of the head. We took fewer individuals of this species at Kâne'ohe Bay than of the other Priolepis species. It usually was found at the outer reefs in deeper water (Greenfield 2003).

MATERIAL EXAMINED.— HAWAIIAN ISLANDS: O'ahu: CAS 218133 (2), CAS 218134 (3), CAS 218135 (1), CAS 218135 (1), CAS 218136 (1), CAS 218137 (1), CAS 218138 (1); BPBM 15456

(4), BPBM 15468 (3), BPBM 19663 (7), BPBM 22625 (2), BPBM 22629 (6), BPBM 35426 (1), BPBM 38477 (1); Midway Atoll: BPBM 22627 (1), BPBM 34783 (1), BPBM 34856 (1), BPBM 34867 (1), BPBM 34942 (1).

***Priolepis limbatosquamis* (Gosline, 1959)**
(Figs. 46 and 78)

Quisquilius limbatosquamis Gosline, 1959, Pac. Sci. 13(1):69, fig. 2. Oahu, Hawaiian Islands. Holotype: USNM 175012. Paratypes: BPBM 14201 [ex UH 1704] (8), additional paratype at USNM.

Diagnosis.— Counts based on 10 individuals 15.0–22.5 mm SL. Dorsal-fin elements VI-I,8-VI-I,9 (VI-I,9). Anal-fin elements I,7-I,8 (I,8). Pectoral-fin rays 17–19 (18). Longitudinal scale series 25–27 (26). Body covered with scales, extending anteriorly at most ¾ of distance to eyes. No scales on opercle or cheek. Interorbital very narrow (less than ½ pupil diameter) but not forming a deep trench between eyes. Pelvic fin longer than wide, reaching anus, frenum completely absent. Jaws extending posteriorly to below anterior margin of pupil. Gill openings extending forward just past edge of preopercle. Caudal fin rounded. Greatest body depth 4.4–4.9 in SL. Largest specimen 28 mm TL.

Figure 78. *Priolepis limbatosquamis*, 30 mm TL, Kâne'ohe Bay, O'ahu, 10 m.

Color in alcohol.— Background color of head and body cream. Scales on body with dark brown margins forming a distinct lattice pattern; scales usually lost leaving only this pattern on scale pockets and no body bars as described in color of fresh adult specimen. Ends of bars often evident on dorsal surface on head and bases of fins. Ventral surface of body cream with peppering of melanophores. Head heavily peppered with melanophores, with a brown bar slightly narrower than pupil diameter under center of eye extending down to posterior end of jaw. A second wider bar extending from posteroventral eye margin across cheek to ventral surface. A third bar running along preopercular margin up and across top of head. A fourth bar extending from pectoral-fin base onto dorsal surface of head. Pectoral and pelvic fins with scattered melanophores on basal membranes, clear distally. Caudal fin with scattered melanophores. Membranes of first and second dorsal fins and anal fin with scattered melanophores.

Color of fresh adult specimen.— (from underwater photograph of freshly captured specimen at Kâne'ohe Bay) Background color of body clear, with six subcutaneous, dark brown bars running from dorsal to ventral surface showing through body: first bar under first dorsal fin; second between first and second dorsal fins; third under anterior portion of second dorsal fin; fourth under center of fin; fifth at end of fin; sixth at center of caudal peduncle. Scales on body with dark brown margins forming a distinct lattice pattern. Ventral surface of belly light cream. Background color of head cream with an orange wash. A distinct orange bar under center of eye extending down to posterior end of jaws. A more diffuse orange bar extending from posteroventral eye margin across cheek to ventral surface. A diffuse orange bar on posterior preopercular margin running onto

top of head. A similar bar extending from pectoral-fin base onto dorsal surface of head. A distinct clear area extending from behind pectoral-fin base onto nape anterior to first dorsal fin. Spines and rays of first and second dorsal fins white with orange spots forming oblique rows, membranes peppered with small, white, iridescent white spots. Caudal-fin rays white with orange spots, forming five or six irregular bars. Basal two-thirds of anal fin orange, distal one-third white. Pectoral and pelvic fins clear.

Color of fresh young specimen.— (from photograph of specimen collected at Kâne'ohe Bay) Background color of head and body clear. Head and body crossed by nine broad brown bands: anteriormost from preopercle across top of head; second across nape anterior to first dorsal fin; third band at anterior portion of first dorsal fin; fourth at posterior end of first dorsal fin; fifth at anterior portion of second dorsal fin; sixth at center of second dorsal fin; seventh at posterior portion of second dorsal fin; eight and ninth bands across caudal peduncle. A red internal band angling posteroventrally from sixth to seventh band (retained from larva). A brown band across head at posterior eye margin and two brown bands under eye. Eye with black pupil, iris silver.

Color of newly settled larva.— (from photograph of specimen collected at Kâne'ohe Bay) Body clear with a distinctive red bar running posteroventrally from middle of second dorsal fin. A red blotch at caudal-fin base. A red line along lower jaw. Red chevron marks on body under pectoral fin. Black on posteriodorsal part of gut showing through body. Eye with black pupil, iris silver.

Distribution.— Hawaiian Islands and Johnston Island.

Remarks.— This is a species that usually is found in the deeper outer part of Kâne'ohe Bay, being most abundant in the deep spur and groove habitat of the bay (Greenfield 2003). It is secretive and not usually seen while diving.

Material examined.— Hawaiian Islands: O'ahu: CAS 218140 (2), CAS 218141 (1), CAS 218142 (1), CAS 218143 (1), CAS 218144 (1), CAS 218145 (1), CAS 218146 (1), CAS 218147 (1), CAS 218148 (2), CAS 218149 (1), CAS 218150 (1), CAS 218151 (2), CAS 218152 (3), CAS 218153 (1), CAS 218154 (1), BPBM 10038 (1), BPBM 17811 (2), BPBM 31016 (1), BPBM 37264 (1); Midway Atoll: BPBM 34802 (1), BPBM 34823 (2), BPBM 34857 (1).

Psilogobius mainlandi Baldwin, 1972

(Figs. 42 and 79)

Psilogobius mainlandi Baldwin, 1972, Pac. Sci. 26(1):126, fig. 4. O'ahu, Hawaiian Islands. Holotype: USNM 206174. Paratypes: BPBM 5522-25 (1, 2, 17, 11), BPBM 10862 (1), BPBM 10864 (26), BPBM 10865 (4).

Diagnosis.— Counts from Watson and Lachner (1985) based on 59 individuals 8.5–37.5 mm SL. Dorsal-fin elements VI-I,9-VI-I,11 (VI-I,10). Anal-fin elements I,8-I,10 (I,9). Pectoral-fin rays 15–19 (16). Longitudinal scale series highly variable, 32–78. Jaws extending posteriorly to or past posterior eye margin. Third (sometimes also second and fourth) dorsal-fin spines elongate, reaching past origin of second dorsal fin when depressed. Pelvic sucking disc longer than wide, reaching or almost reaching anal-fin origin. Pelvic-fin frenum very well-developed, extending to ends of pelvic spines (about one-third to one-half of fin length). Body covered with small scales that are partially embedded anteriorly near pectoral-fin base. No scales on head or nape. Gill openings extending forward to preopercular margin. Interorbital narrow, less than one pupil diameter. Caudal fin broad and pointed, as long as or a little longer than head length. Greatest body depth 5.0–7.1 in SL. Attains 58 mm TL.

Color in alcohol.— Background color of head and body light cream. Body with a series of 10 midlateral brown blotches of varying sizes extending from pectoral-fin base to caudal-fin base.

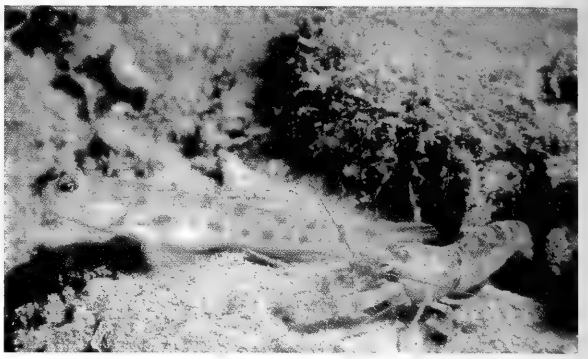

FIGURE 79. *Psilogobius mainlandi*, 35 mm TL, and *Alpheus rapax*, Kâne'ohe Bay, O'ahu, 2 m.

Six blotches are larger with smaller blotches in between larger blotches. A second series of brown blotches along dorsal side of body at fin bases. Six of these blotches larger and extend into fin bases: two under first dorsal fin, three under second dorsal fin, and sixth on caudal peduncle. Five smaller brown spots spaced between larger spots, not crossing back. A brown band, about width of pupil across nape above pectoral-fin base. Pectoral-fin base with a light brown blotch on upper half. Cheek with a brown bar from top of upper jaw to top of preopercular margin. A second bar from ventral margin of center of eye forward onto upper jaw. Top of head with two brown blotches in advance of band on nape. Pectoral, pelvic, and anal fins with scattered melanophores. First dorsal fin with scattered melanophores on membranes, with extension of large body spots onto basal portion of fin. Dorsal spots also extending onto basal portion of second dorsal fin. Branchiostegal membranes black in males.

COLOR IN LIFE.— (from underwater photograph of living fish at Kâne'ohe Bay) Background color of head and body grayish white, ventral surface lighter. Small, iridescent blue spots scattered over head and body. Five distinct, vertical, white lines on side of body: first three under first dorsal fin; remaining two under anterior portion of second dorsal fin; all except last under pectoral fin. A series of six dark orange-brown blotches along midline of body: first between first two white lines; second between lines four and five, remaining posterior spots evenly spaced along side with last one at caudal-fin base. Corresponding dark brown blotches dorsal to those at midline, running along dorsal-fin bases. An orange-brown blotch at center of pectoral-fin base. Another blotch anterior to that blotch on opercle. Side of head with a dark brown line from posterior end of jaws to top of opercle. A dark brown line from upper jaw to anteroventral margin of eye. Pectoral fins clear. Pelvic fins dusky, posterior margin dark brown. First and second dorsal fins dusky with scattered, small, iridescent blue spots on basal third of fins. Second dorsal fin with an iridescent blue margin. Caudal fin dusky with a yellowish tinge, a few small iridescent, blue spots on central rays, and iridescent blue margin.

DISTRIBUTION.— Hawaiian Islands.

REMARKS.— This species lives in shallow, protected areas on silty sand. It has a symbiotic relationship with the snapping shrimp, *Alpheus rapax*, living in the burrow usually with a pair of shrimp. The shrimp build and maintain the burrow, and the goby, with its superior vision and lateralis system, serves as the sentinel. When the shrimp emerge to deposit sediment or repair the burrow entrance, they usually make contact with the goby with one of their antennae. In return, the goby is provided with a home and perhaps food that is pushed up by the shrimp.

MATERIAL EXAMINED.— HAWAIIAN ISLANDS: O'ahu: CAS 218156 (14), CAS 218157(3), CAS 218158 (2), 62 BPBM paratypes listed above, BPBM 22624 (4), BPBM 22644 (1), BPBM 31323 (43); Maui: BPBM 32844 (1).

Trimma milta Winterbottom, 2002

(Fig. 80)

Trimma milta Winterbottom, 2002, Aqua, Jour. Ichthyology and Aquatic Biol. 5(2):45–52. Moorea, Society Islands. Holotype: ROM 59750. Paratypes: BPBM 8617 (5), BPBM 9410 (2), other paratypes at various museums.

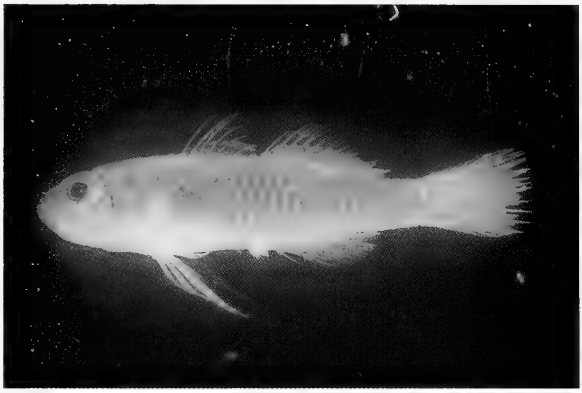

FIGURE 80. *Trimma milta*, BPBM 38706, 18.7 mm SL, Pûpûkea, O'ahu, 23 m.

DIAGNOSIS.— Dorsal-fin elements VI-I,9. Anal-fin elements I, 8. Pectoral-fin rays 17–18 (usually 17). Longitudinal scale series 22–24. Predorsal scales 6–8. Ctenoid scales on body extending a little anterior to origin of first dorsal fin; nape, opercle, pectoral-fin base, chest, and midline of abdomen with cycloid scales, those on opercle in a single dorsal row (may be absent in juveniles). Pelvic fins united by membrane only basally, the membrane one-tenth length of fifth pelvic rays; fin longer than wide, extending at least to anal-fin origin; fifth pelvic ray unbranched and only about half length of longest pelvic ray; no pelvic frenum. Gill opening extending forward to pupil. Jaws extending posteriorly to below front of pupil. Interorbital slightly wider than one-half pupil diameter. Caudal fin slightly rounded. Greatest body depth 4.0–4.5 in SL. Largest specimen 28 mm TL.

COLOR IN ALCOHOL.— Head and body cream. Scale pockets with dark brown pigment at edges so scales strongly outlined on body. Head and pectoral-fin base peppered with very small dark brown pigment spots. Pupil of eye cream, iris black. Spines and rays of dorsal and anal fins with orange-brown pigment, some similar pigment on fin membranes towards base of fins. Pectoral, pelvic, and caudal fins clear.

COLOR IN LIFE.— (from photograph of live specimen from Pûpûkea, O'ahu taken by R.R. Holcom-BPBM 38706 also Fig. 4 in Winterbottom, 2002) Head and body orange-red. Scale pockets rimmed with dark brown pigment so scales strongly outlined on body, making body darker than head. Pupil of eye black, surrounded by a yellow ring. Iris dusky yellow with neon blue pigment above and below pupil. Fin rays of both dorsal, anal, and pectoral fins orange-red, membranes clear. Caudal fin yellowish.

DISTRIBUTION.— Reported from Society Islands, Hawaiian Islands, Marshall Islands, Caroline Islands, Fiji, Solomon Islands, Great Barrier Reef, Papua New Guinea, Indonesia, Philippines, Taiwan, and western Australia.

REMARKS.— Specimens have been collected from depths of 9–29 m from coral reefs and sand-rubble substratum. Our only Hawaiian specimen (BPBM 38706) was collected on O'ahu off Hale'iwa (N.W. side of Pûpûkea reef) in 23 m of water under ledges and in small holes at a dropoff by R.R. Holcom. Holcom reported that the species was sometimes in pairs, side by side.

Trimma taylori Lobel, 1979

(Fig. 81)

Trimma taylori Lobel, 1979, Breviora (456):3, fig. 1. Oahu, Hawaiian Islands. Holotype: BPBM 19919. Paratypes: BPBM 19920 (1), BPBM 19921 (2), BPBM 19922 (8).

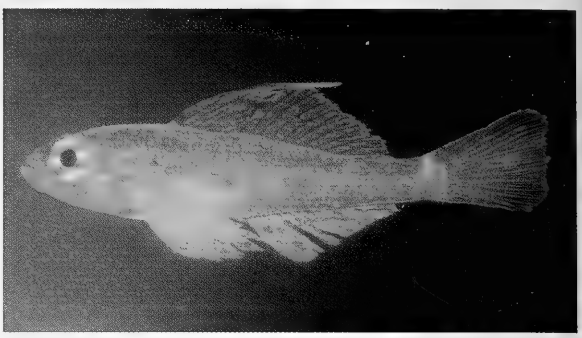

FIGURE 81. *Trimma taylori*, 23 mm TL, Waikiki Aquarium, Honolulu.

DIAGNOSIS.— Dorsal-fin elements VI-I,10-11 (rarely 11). Anal-fin elements I,9-10 (rarely 9). Pectoral-fin rays 13–15. Longitudinal scale series 23–24 (usually 24). Predorsal scales 6–8. Head naked, scales on body ctenoid, becoming cycloid on pectoral-fin base, chest, and ventrally on abdomen. Second dorsal spine elongate and filamentous, sometimes the third as well. Pelvic fins united by membrane for about one-third length of fins; fin longer than wide, usually extending to base of third anal soft ray; fifth pelvic ray branched, about four-fifths length of fourth ray; no pelvic frenum. Gill opening extending forward to below pupil. Jaws extending posteriorly to below front of eye. Interorbital about as wide as pupil diameter. Caudal fin truncate. Greatest body depth 4.4–5.6 in SL. Reaches 25 mm TL.

COLOR IN ALCOHOL.— Head, body, and fins all cream colored, no dark pigment in preserved material.

COLOR OF FRESH SPECIMEN.— (from photographs taken at Kona and Kan'eohe Bay) Body and head translucent pale yellow or pale red. Backbone visible through body with alternating black and white sections on top; these alternating sections extending down below midline on anterior half of body. Head yellow dorsally behind eyes, overlaid by small reddish brown spots; a white bar in this area crossing between eyes. Eye with black pupil, surrounded by golden iris that has reddish blotches on it. Surface of body, head, and fins covered with tiny yellow spots.

DISTRIBUTION.— Red Sea, Chagos Archipelago, and Maldive Islands to Hawaiian Islands, and Society Islands.

REMARKS.— Generally found in caves or under ledges, mostly in 20–50 m, often in small aggregations above the bottom. Named from O'ahu for Leighton Taylor, former director of the Waikiki Aquarium.

MATERIAL EXAMINED.— HAWAIIAN ISLANDS: O'ahu: CAS 218159 (1), BPBM 31038 (9), BPBM holotype and three paratypes listed above.

Trimma unisquamis (Gosline, 1959)

(Figs. 47, 48, and 82)

Hazeus unisquamis Gosline, 1959, Pac. Sci. 13(1):70, fig. 3. O'ahu, Hawaiian Islands. Holotype: USNM 175009.

DIAGNOSIS.— Counts based on 20 individuals 13.3–17.1 mm SL. Dorsal-fin elements VI-I,6-7 (VI-I,7). Anal-fin elements I,6-7 (I,7). Pectoral-fin rays 18–19 (19). Longitudinal scale series 24–25. A dark band at caudal-fin base. Both dorsal fins with a black border. Pelvic sucking disc longer than wide, reaching anal-fin origin; frenum well developed. Body covered with scales extending forward onto top of head to eyes. Scales on opercle but not cheek. Gill membranes not fused to isthmus, gill opening extending forward to below anterior margin of eye. Jaws extending posteriorly to mid pupil. Interorbital space very narrow, less than one pupil diameter. Caudal fin truncate. Greatest body depth 4.0–4.3 in SL. Attains about 26 mm TL.

COLOR IN ALCOHOL.— Background color of head and body cream. Dorsal half of body, nape, and sides of head overlaid with scattered melanophores. A distinct dark brown bar at caudal-fin

base. Eye with black pupil surrounded by silver iris, edged with black. Pectoral, pelvic, and anal fins lacking pigment. Caudal fin clear with dusky area on distal one-third. First and second dorsal fins with scattered melanophores and black distal margins.

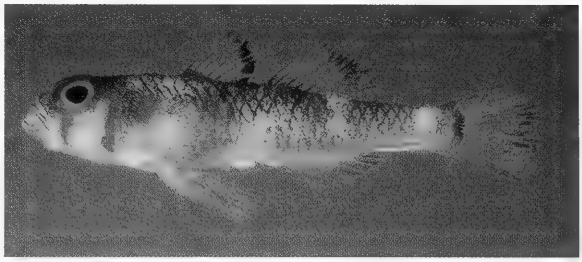

FIGURE 82. *Trimma unisquamis*, BPBM 37265, 18.5 mm SL, Kâne'ohe Bay, O'ahu, 12 m.

COLOR OF FRESH SPECIMEN.— (from photograph of freshly collected specimen from Kâne'ohe Bay) Background color of body lemon yellow. Dorsal half of body and nape overlaid by diffuse black pigment, somewhat more concentrated on scale margins. A distinct black bar at caudal-fin base. Background color of head red, overlaid by dusting of melanophores. Eye with black pupil surrounded by golden ring, iris red. Pectoral and pelvic fins yellow. First dorsal fin with reddish orange spines, membranes on basal three-quarters clear, distal one-quarter black. Some black pigment on membranes at bases of spines one through four. Second dorsal fin with same color pattern as first. Anal fin yellow with some black pigment distally. Caudal fin yellow, anterior dorsal and ventral margins red, distal half of fin dusky.

DISTRIBUTION.— Hawaiian Islands, Easter Island, Society Islands, Tonga, and Guam.

REMARKS.— This species typically is found in more open offshore reefs, being most abundant in the deep spur and groove habitat at Kâne'ohe Bay (Greenfield 2003).

MATERIAL EXAMINED.— HAWAIIAN ISLANDS: O'ahu: CAS 218160 (18), CAS 218164 (43), CAS 218161 (12), CAS 218163 (46), BPBM 22653 (1), BPBM 37265 (4); Maui: BPBM 14208 (1); Midway Atoll: BPBM 34824 (7).

DISCUSSION

Several small specimens (about 14 mm SL) of a goby (CAS 218162) were taken at Kahana Bay, O'ahu in 1990 while seining with the University of Hawaii ichthyology class. We could not identify the specimens and thus sent them to Helen Larson in Australia, who placed them in the genus *Favonigobius*. This genus is not known from Hawaii, and thus is most likely an introduction, perhaps through bilge water. Attempts to collect more specimens were not successful, and it is not known if it has become established. This species keys to 28a in our key (*Priolepis*), but it clearly is not within that genus. Whereas *Priolepis* species have horizontal rows of papilla across the cheek and above the upper jaw, they are lacking in *Favonigobius*. In addition, the mouth is much more oblique in *Priolepis* than in *Favonigobius*. A drawing of one of the *Favonigobius* specimens is presented (Fig. 83) to aid in its identification if future specimens are collected.

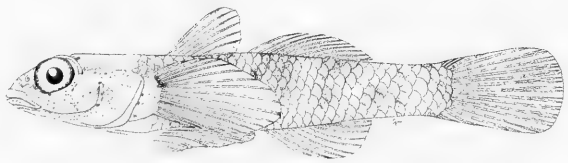

FIGURE 83. *Favonigobius* sp., CAS 218162, 13.5 mm SL, Kahana Bay, O'ahu, less than 0.5 m.

ACKNOWLEDGMENTS

We would like to thank the following persons for assistance in collecting gobies in Hawai'i: Erin Baumgartner, Nancy C. Burke, Geoffrey J. Cockrell, Kathleen S. Cole, David B. Eckert,

Ronald R. Holcom, Robert K. Johnson, Ross C. Langston, Kenneth R. Longenecker, and Jeffrey L. Mahon. Robert B. Moffitt provided us with deep-water specimens of *Opua*. Jennifer K. Schultz and Brian R. Bowen compared deep and shallow water *Opua* populations using DNA. We thank the personnel of the Division of Aquatic Resources of the Hawai'i Department of Land and Natural Resources for granting permission to collect fishes using ichthyocides. Susan G. Monden drew all of the figures, and we thank her for this. We thank Helen A. Randall for her assistance in editing. This research was supported by grant no. R/E1-5PD from Sea Grant.

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Two New Species of Dorid Nudibranchs (Mollusca, Opisthobranchia) from Bahía de Banderas and La Paz, Mexico

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Two new species of dorid nudibranchs from the Pacific coast of Mexico are described based on specimens collected from Bahía de Banderas and one specimen from La Paz. *Trapania goddardi* sp. nov. is most similar to *Trapania goslineri* (Millen and Bertsch, 2000) and *Trapania inbiotica* (Camacho and Ortea, 2000), but it is differentiated by the absence of yellow markings on the extra-rhinophoral and extra-branchial processes and the presence of marginal, large cusps on the radular teeth. *Paradoris lopezi* sp. nov. is characterized by a pale grayish-tan background color with reddish tubercles. This species is differentiated from other species of *Paradoris* from the Pacific Ocean by the presence of the external coloration mentioned above, the presence of two accessory glands and a single accessory sac with a spine, and the number and morphology of radular teeth and jaw elements.

KEY WORDS: Goniodorididae, Discodorididae, Tropical eastern-Pacific.

RESUMEN

Dos especies nuevas de dóridos nudibranquios son descritas para la costa Pacífica de México, en base a espécimenes recolectados en Bahía de Banderas y un espécimen en La Paz. Las especies más similares a *Trapania goddardi* esp. nov. son *Trapania goslineri* (Millen y Bertsch, 2000) y *Trapania inbiotica* (Camacho y Ortea, 2000), pero se diferencian por la ausencia de manchas amarillas en los apéndices extra-branquiales y extra-rinofóricos, y por la presencia de cúspides marginales en los dientes de la rádula. *Paradoris lopezi* esp. nov. se caracteriza por tener una coloración general grisáceo pardo claro con tubérculos rojizos. Esta especie se diferencia de otras especies de *Paradoris* del Océano Pacífico por la coloración externa antes mencionada, la presencia de dos glándulas accesorias y un saco accesorio con una espina, así como por el número y forma de los dientes radulares, y de los elementos de la armadura labial.

PALABRAS CLAVE: Goniodorididae, Discodorididae, Pacifico Este tropical.

There has been a significant lack of information on the diversity and opisthobranch faunal composition in Bahía de Banderas, Mexico. Only a few papers have been published on the opisthobranchs from the northern coast of the bay, situated in the state of Nayarit (Sphon and Mulliner 1972; Bertsch et al. 1973; Bertsch 1978, 1980; Bertsch and Kerstitch 1984; Ferreira and Bertsch 1975), and Isla Isabel (Ortea and Llera 1981); and there are no published studies on the opisthobranchs from the central and southern sections of the bay, in the state of Jalisco.

A recent survey by the senior author has revealed a diverse opisthobranch fauna in Bahía de Banderas, including numerous undescribed species (Hermosillo-González 2003). Ninety-six species represented by over 20,000 specimens were identified in the field or collected, including 20 new records for this area, revealing a previously undocumented diverse fauna. In this paper we describe two new species collected during the survey.

Materials and Methods

Most of the material examined was collected in several localities in Bahía de Banderas, Mexico, by the senior author. Bahía de Banderas is located on the west coast of México, in the states of Jalisco and Nayarit. Its large surface, over 1,000 km^2, makes it the largest bay along the Pacific coast of mainland México. Punta Mita and Cabo Corrientes, 42 kilometers apart, delimit Bahía de Banderas to the north and south respectively.

The specimens are deposited at the Department of Invertebrate Zoology and Geology of the California Academy of Sciences, San Francisco (CASIZ) and the Malacology Section of the Natural History Museum of Los Angeles County (LACM). Specimens were dissected and the internal features were examined and drawn using a dissecting microscope with a camera lucida. A portion of the mantle was critical-point dried for the Scanning Electron Microscope (SEM). The buccal mass was removed and dissolved in 10% sodium hydroxide until the radula was isolated from the surrounding tissue. The radula was then rinsed in water, dried, and mounted for examination with the SEM. Features of living animals were recorded from field photographs by the senior author.

Species Descriptions

Family Discodorididae Bergh, 1891

Genus *Paradoris* Bergh, 1884

Type species: *Paradoris granulata* Bergh, 1884, by monotypy.

***Paradoris lopezi* Hermosillo and Valdés, sp. nov**
(Figs. 1A–B, 2–3)

Material Examined.— Holotype: Punta de Pichilingue (24°21.25′N 110°17.001′W), La Paz, Baja California Sur, Mexico, 31 October 2004, 1 specimen 32 mm long, collected under coral rubble at 1 m depth (CASIZ 171661). Paratype (1): Majahuitas (20°29.111′N 105°35.057′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 10 March 2004, 27 mm long, collected under a rock at 12 m depth (LACM 3041).

External morphology.— The maximum length of the living animal is 32 mm. The preserved holotype measures 22 × 12 mm. The body shape is oval with an irregular mantle margin. The notum is larger than the foot, covering it completely (Figs. 1A–B). The gill is composed of 7 tripinnate leaves and is retractable into an irregular sheath, which is slightly inclined posteriorly. The anus is located in the middle of the branchial plume. The rhinophores have 15 conspicuous lamellae and are retractable into irregular sheaths. The dorsum is porous and lacks caryophyllidia (Fig. 2E), but it is covered with irregular tubercles of different sizes. There are a few larger tubercles on the center of the dorsum and smaller and more abundant tubercles towards the mantle margin. Minute tubercles cover the entire surface of the dorsum. Ventrally, the anterior border of the foot is notched and grooved. The oral tentacles are conical and not grooved.

The color of the body is pale grayish-tan with the smaller tubercles having the same color as the rest of the body (Fig. 1A). On closer inspection, minute dark ringlets composed of black specks

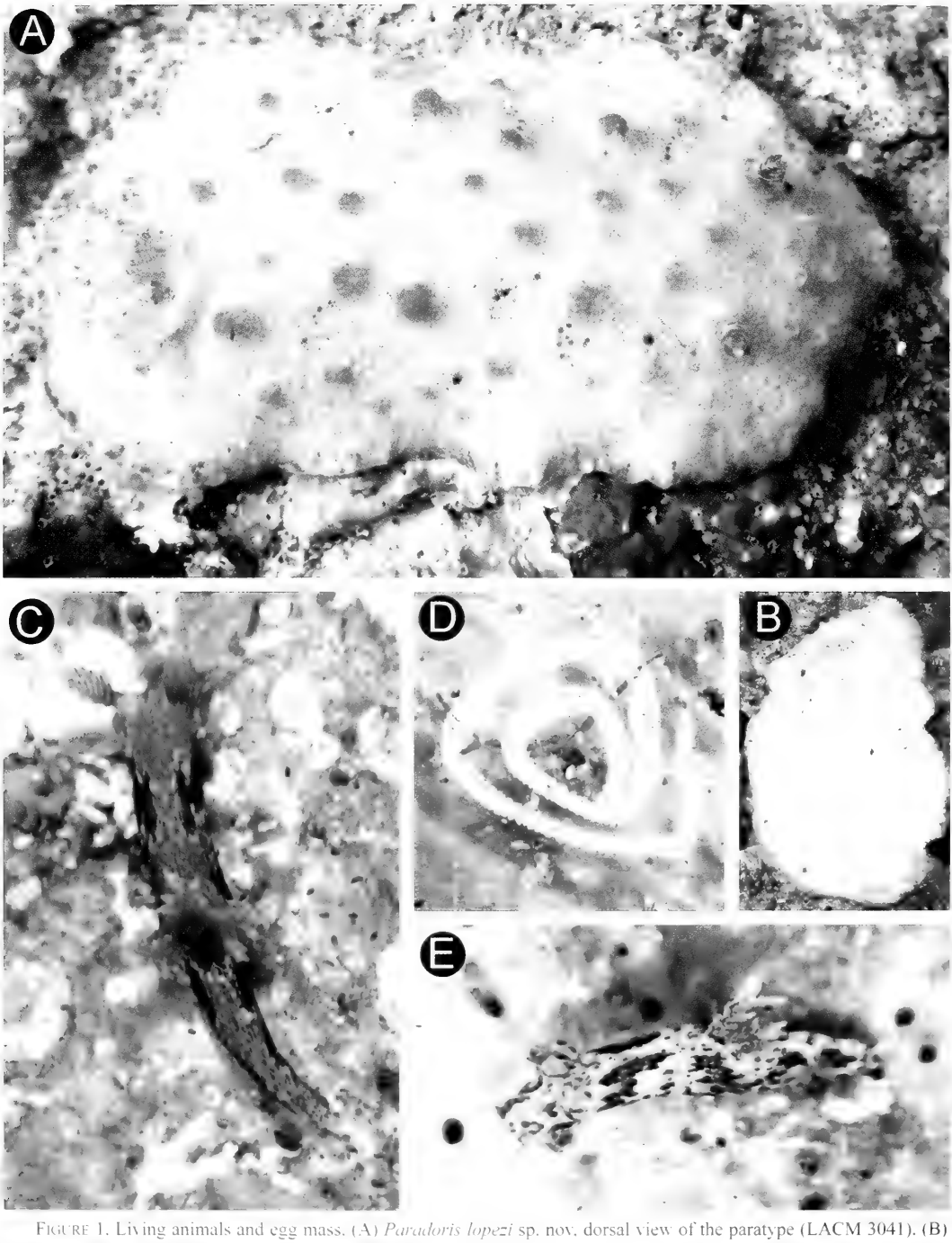

FIGURE 1. Living animals and egg mass. (A) *Paradoris lopezi* sp. nov, dorsal view of the paratype (LACM 3041). (B) Same specimen, ventral view. (C) *Trapania goddardi* sp. nov, holotype (LACM 3039). (D) *Trapania goddardi* sp. nov, egg mass. (E) *Trapania goddardi* sp. nov, lighter paratype (CASIZ 171662).

and white flecks can be observed. A few irregularly distributed large black spots can be observed on the dorsum. The larger tubercles in the center of the dorsum are of a dark reddish-orange. The mantle margin is encircled by a blotchy tan line. The branchial leaves are clear grayish-tan with darker tips. The rhinophores have a clear stalk with dark lamellae. The ventral side of the body is white with a few tan spots; color varies among individuals from pale to dark grayish-tan.

Internal Anatomy.— The oral tube is small and short, with six strong retractor muscles attached posteriorly (Fig. 3C). The buccal bulb is about twice as large as the oral tube, rounded, with a conspicuous radular sac emerging from the posterior ventral surface and pointing upwards. There is a pair of retractor muscles attached to the sides of the buccal bulb. There are two elongate and folded salivary glands attached to the buccal mass, near the esophageal insertion.

The radular formula is 23 × 17.0.17 in a 27 mm long specimen (LACM 3041). There is no rachidian tooth. The innermost lateral teeth are simple hooks with a long, curved cusp and no denticles (Fig. 2A). The mid-lateral teeth change abruptly in size, becoming larger at about teeth 3–4; the cusps of the mid-lateral teeth are also shorter and the base longer and more curved than those of the inner teeth (Fig. 2B). The outer teeth are smaller and have a short triangular cusp; the outermost tooth of each row is reduced to a simple plate (Fig. 2C). The labial cuticle has a pair of jaws composed of numerous, irregular rodlets (Fig. 2D).

Reproductive system.— The reproductive system is triaulic (Figs. 3A–B). The narrow preampullary duct widens into a long and convoluted ampulla that has three folds. The ampulla narrows abruptly into the distal portion and connects to the female glands and the prostate. The prostate is broad, glandular and folded, with two regions clearly differentiated. The prostate narrows into the deferent duct, which is a long, extremely narrow and irregularly coiled tube that opens in a large common atrium with the vagina. The penis is unarmed. The vagina is a long, thin tube that tapers proximally and runs over the female gland to enter the large, spherical bursa copulatrix. The seminal receptacle is rounded and connects serially to the bursa copulatrix.

Geographic range.— This species is only known from Bahía de Banderas, Jalisco-Nayarit, Mexico and La Paz, Baja California Sur, Mexcio.

Natural History.— This species is found in the shallow subtidal (12 m depth) under rocks. Individuals produce a milky substance when disturbed.

Etymology.— The specific name is dedicated to the memory of the father of the second author, Ángel Valdés López, who passed away in August 2003.

Remarks.— *Paradoris lopezi* has all the features characteristic of the genus *Paradoris* (see Valdés 2002) as follows: anterior border of the foot notched and grooved; dorsum covered with simple tubercles, stiffened by integumentary spicules; labial cuticle armature with rodlets; radula composed of simple, strong, hamate teeth, which have a short cusp and lack denticles; reproductive system with a flattened, granular prostate, having two well differentiated regions, and a series of accessory glands and/or accessory sacs containing copulatory spines; penis and vagina devoid of hooks.

Four other species of *Paradoris* are known from the Pacific Ocean, but none has previously been reported from the eastern Pacific. These four species are: *Paradoris leuca* Miller, 1995 from New Zealand, *Paradoris tsurugensis* Baba, 1986, from Japan, and *Paradoris araneosa* Valdés, 2001 and *Paradoris imperfecta* Valdés, 2001, both from New Caledonian deep waters.

Paradoris leuca differs from *P. lopezi* by lacking accessory glands and copulatory sacs armed with spines (see Miller 1995). Other differences are the shape of the jaw elements, which have a triangular cusp in *P. leuca* and are rounded or irregular in *P. lopezi*. Externally, the dorsal tubercles of *P. leuca* are smaller than those of *P. lopezi*.

Paradoris tsurugensis is the most similar species to *P. lopezi* in external morphology and col-

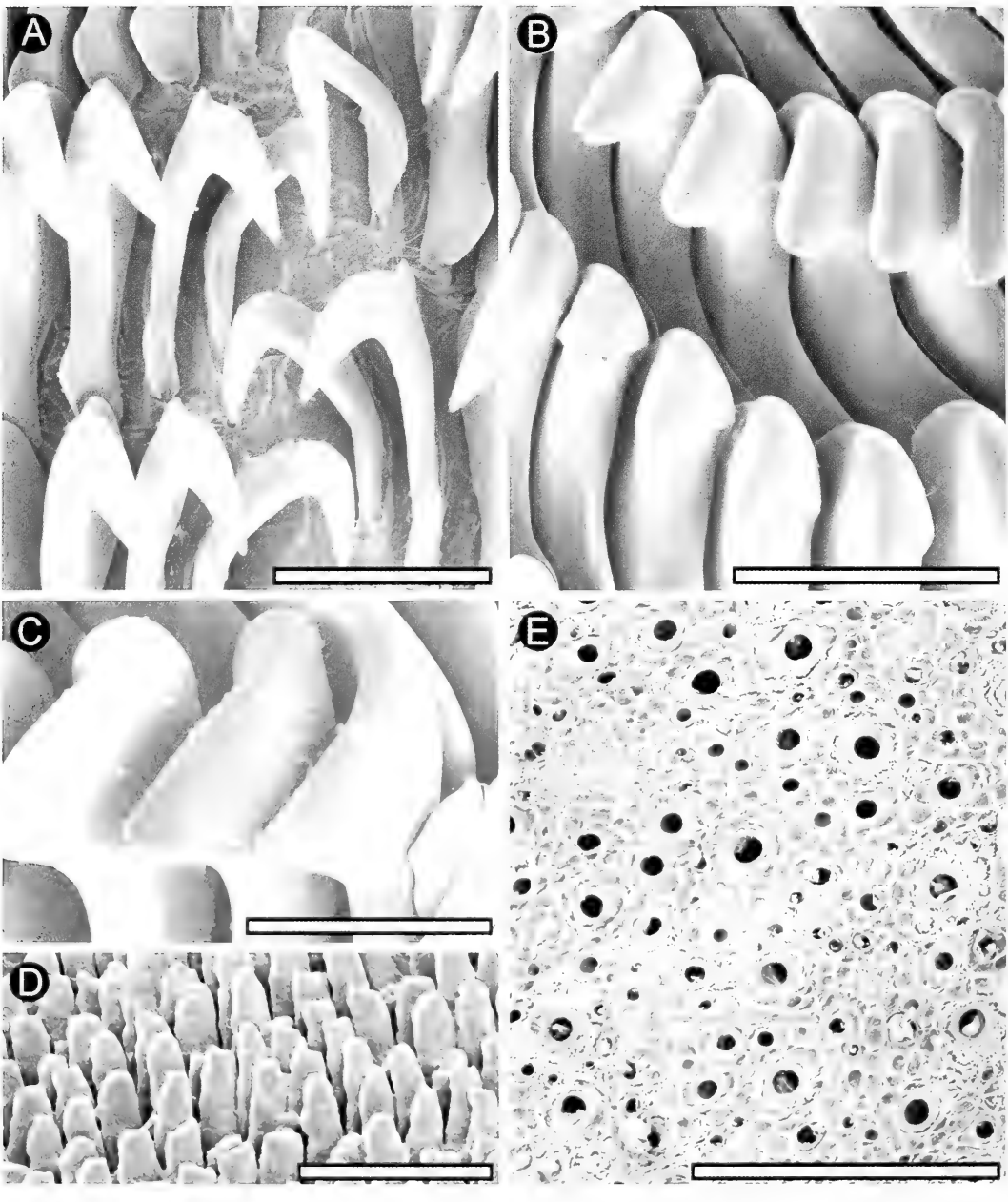

FIGURE 2. *Paradoris lopezi* sp. nov., paratype (LACM 3041). Scanning Electron Micrographs of radula, jaws, and dorsum. (A) Innermost lateral teeth, scale bar = 100 µm. (B) Mid-lateral teeth, scale bar = 100 µm. (C) Outermost lateral teeth, scale bar = 50 µm. (D) Jaw rodlets, scale bar = 30 µm. (E) Dorsum, scale bar = 500 µm.

oration. Both species share a grayish background color with large yellowish-orange dorsal tubercles. However, the tubercles of *P. tsurugensis* are lighter than those of *P. lopezi*, and in the former species they are surrounded by a darker line and often have a darker central area. The tubercles of *P. lopezi* are uniformly dark reddish-orange. Anatomically, *P. tsurugensis* is distinguishable from *P.*

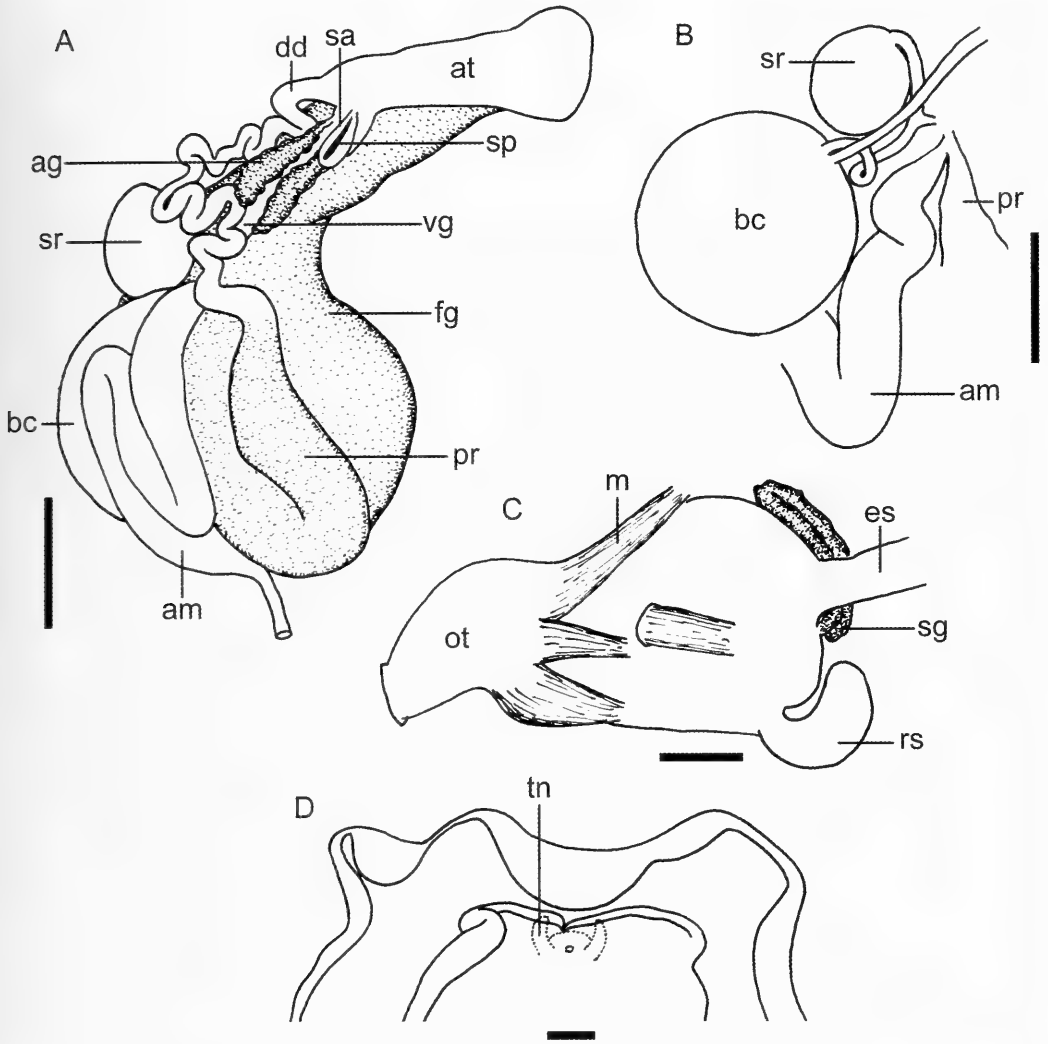

FIGURE 3. *Paradoris lopezi* sp. nov, paratype (LACM 3041), anatomy. (A) Reproductive system, scale bar = 1 mm. (B) Detail of several reproductive organs, scale bar = 1 mm. (C) Lateral view of the buccal mass, scale bar = 1 mm. (D) Ventral view of the anterior end of the foot, scale bar = 1mm. Abbreviations: am, ampulla; at, genital atrium; ag, accessory gland; bc, bursa copulatrix; dd, deferent duct; es, esophagus; fg, female glands; ot, oral tube; pr, prostate; sg, salivary gland; rs, radular sac; sa, accessory sac; sp, copulatory spine; sr, seminal receptacle; tn, oral tentacle; vg, vagina.

lopezi in having two accessory glands and two copulatory sacs armed with spines (see Baba 1986), instead of two accessory glands and a single accessory sac. Also, *P. tsurugensis* has many more radular teeth than *P. lopezi* at comparable size. The radular formula of the former is 90 × 20-25.0.20-25 whereas it is 23 × 17.0.17 in the latter.

Paradoris araneosa is clearly distinguishable from *P. lopezi* by its external morphology and coloration. The dorsal tubercles or *P. araneosa* are smaller and more densely arranged than those of *P. lopezi*. Additionally, the color of the former is pale brown with a few large, dark brown spots scattered on the dorsal surface, and several, more numerous, small darker dots; the larger tubercles

are opaque white. This contrasts with *P. lopezi*, which is pale grayish-tan with the smaller tubercles having the same color as the rest of the body and the larger tubercles being dark reddish-orange.

Paradoris imperfecta differs from *P. lopezi* in lacking accessory glands and by having two accessory sacs (see Valdés 2001), instead of one. Externally, *P. imperfecta* lacks the large dorsal tubercles present in *P. lopezi*. Also, the color of the living animals is uniformly cream with a few, irregular, pale brown spots, and numerous small dark brown dots on the dorsal surface, which is very different from the pale grayish-tan color with dark reddish-orange tubercles of *P. lopezi*.

Family Goniodorididae H and A. Adams, 1854

Genus *Trapania* Pruvot-Fol, 1931

TYPE SPECIES: *Trapania fusca* (Lafont, 1874), by monotypy.

Trapania goddardi **Hermosillo and Valdés, sp. nov**
(Figs. 1C-E, 4-5)

MATERIAL EXAMINED.— HOLOTYPE: Islas Marietas (20°42.042′N, 105°33.878′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 17 April 2003, 7 mm long, collected on a wall at 9 m depth (LACM 3039). PARATYPES (2): Islas Marietas (20°42.042′N, 105°33.878′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 17 April 2003, 1 specimen 6 mm long, dissected (CASIZ 171662); Bajo de la Viuda (20°43.973′N, 105°23.544′W), Bahía de Banderas, Jalisco-Nayarit, Mexico, 18 November, 2003, 1 specimen 3 mm long collected on a wall at 12 m of depth, dissected (LACM 3040).

EXTERNAL MORPHOLOGY.— The maximum length of the living animal is 7 mm. The body is smooth, lacking tubercles, and elongate, wider in the middle region (Figs. 1C–E). The border of the mantle is reduced, undifferentiated. Each side of the body bears a digitiform extra-branchial process and a digitiform and posteriorly-curved extra-rhinophoral process. The non-retractile rhinophores are short and stout; they have no sheaths and bear 6–7 lamellae. The three branchial leaves are bipinnate and non-retractile. The anus closes the branchial circlet posteriorly. The digitiform oral tentacles are short, situated antero-laterally on the rounded cephalic region.

The color of the body is variable from off-white with irregular small brown blotches on the middle and sides of the dorsum to tan with darker blotches. The larger blotches are almost diamond shaped; the two anterior ones join in the middle of the dorsum. The density of the brown blotches can vary between individuals (Figs. 1C–E). The ventral side of the body is off-white. The oral tentacles, rhinophores, branchial leaves, posterior end of the foot, and extra-branchial and extra-rhinophoral processes are the same color as the rest of the body, off-white with some brown spots.

INTERNAL ANATOMY.— The radular formula is 17 × 1.0.1 in a 6-mm long specimen (LACM 3040). The radula consists of two series of 17 elongated lateral teeth (Fig. 4A). Each tooth has a long, sharp, hamate cusp displaced to the side of the radula, which generally curves inwards. Additionally, each tooth has a series of 4–6 large denticles with 1–3 smaller denticles intercalated between the larger ones.

The jaws have a single series of rodlets on the masticatory border (Fig. 4B); they have a single cusp and a wide base.

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 5A). The ampulla is pyriform and connects directly to the female gland and prostate. The prostate is wide and irregular in shape, with a single loop; it connects to the deferent duct, which opens into a common atrium with the vagina. The long, narrow vagina connects directly to the rounded bursa copulatrix (serial) near the insertion point of the smaller, round, seminal receptacle. The penis bears several rows of penial hooks of different sizes and shapes (Fig. 5B).

Geographic range.— *Trapania goddardi* is known from the type locality in Bahía de Banderas, Jalisco-Nayarit and from Santa Cruz, Nayarit, Mexico.

Natural History.— This species is found intertidally and in the upper subtidal (maximum depth 12 m) on or under rocks. The cryptic coloration, which blends with the environment, and its small size make this species difficult to find. The egg mass is a clear string of large white eggs with two whorls (Fig. 1D). The size of the egg mass is 6.3 mm × 5.4 mm with an average width of 0.76

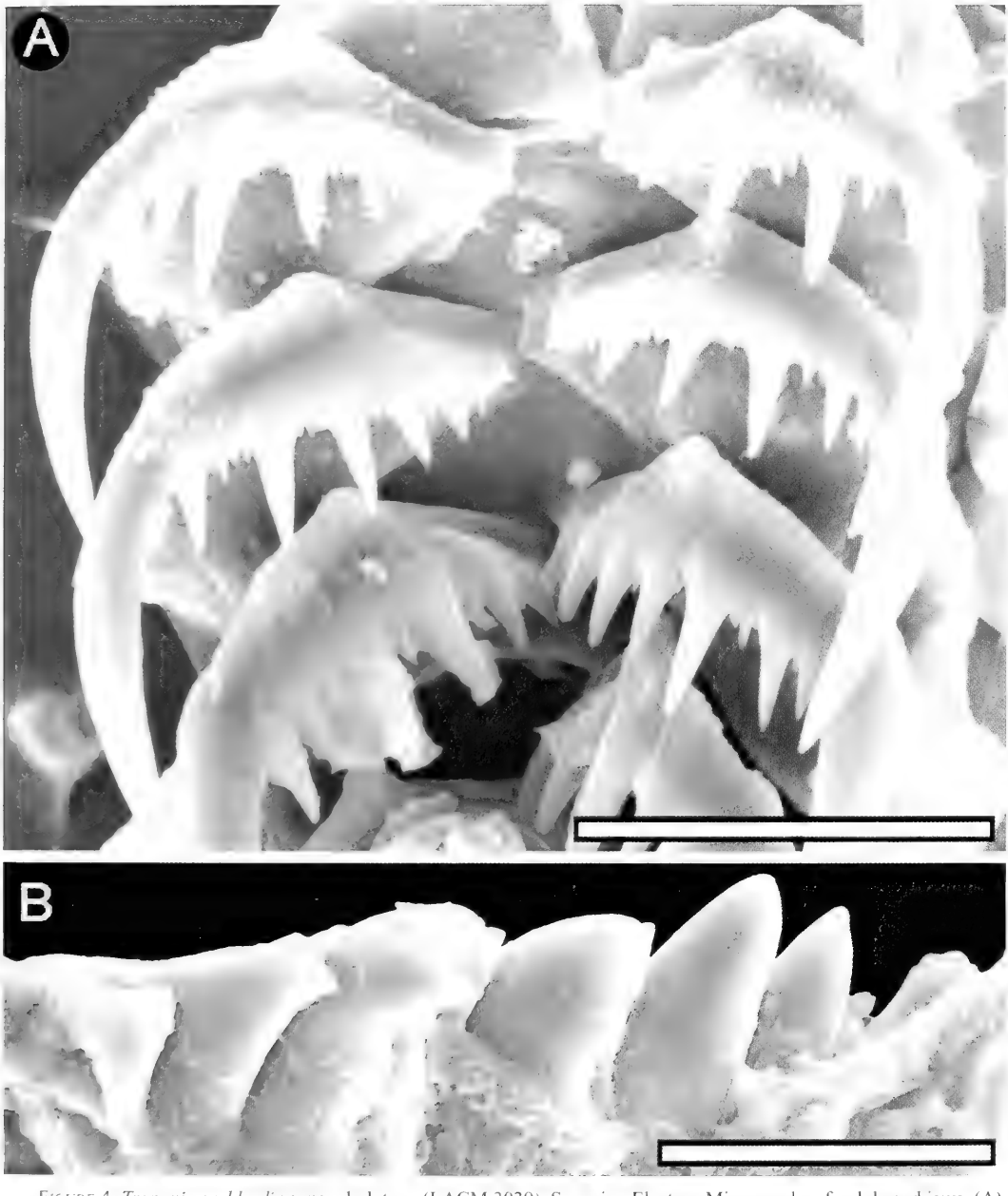

Figure 4. *Trapania goddardi* sp. nov, holotype (LACM 3039), Scanning Electron Micrographs of radula and jaws. (A) Radular teeth, scale bar = 20 μm. (B) Jaw rodlets, scale bar = 20 μm.

mm. The average diameter of the eggs is 0.135 mm. The average number of eggs per square mm is 56.

Etymology.— The specific name is given in honor of Dr. Jeff Goddard who first found this species in 1985.

Remarks.— The generic placement of *Trapania goddardi* is based on the shape of the body, which is elongate, wider in the middle, with a pair of extra-branchial and a pair of extra-rhinophoral processes; the radular morphology is also diagnostic with a single series of elongate lateral teeth with several pointed denticles and a larger outer cusp, and lacking a rachidian tooth.

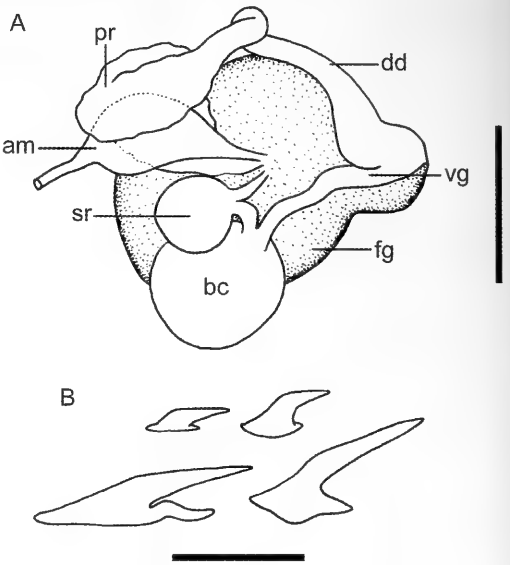

FIGURE 5. *Trapania goddardi* sp. nov, holotype (LACM 3039), anatomy. (A) Reproductive system, scale bar = 0.5 mm. (B) Penial spines, scale bar = 10 µm. Abbreviations: am, ampulla; bc, bursa copulatrix; dd, deferent duct; fg, female glands; pr, prostate; sr, seminal receptacle; vg, vagina.

There are three valid species of *Trapania* described for the eastern Pacific: *Trapania velox* (Cockerell, 1901) is known from California to the Pacific side of Baja California (Behrens 2004); *Trapania goslineri* Millen and Bertsch, 2000, is known from the Gulf of California, the outer coast of Baja California, and from the Pacific Coast of mainland Mexico in Bahía de Banderas (Hermosillo-González 2003); and *Trapania inbiotica* Camacho and Ortea, 2000 is known only from Costa Rica (Camacho and Ortea 2000). *Trapania goslineri* alone has been reported for an area that overlaps the known range of *T. goddardi*.

The three eastern Pacific species have a bright white background color and are easily distinguishable from *T. goddardi*. Both *T. velox* and *T. goslineri* have yellow markings on the oral tentacles, rhinophores, branchial leaves, extra-rhinophoral and extra-branchial processes, and on the dorsal portion of the posterior part of the foot (Millen and Bertsch 2000). Similar yellow markings can be observed in *T. inbiotica* except for the branchial leaves and rhinophores (Camacho and Ortea 2000). *Trapania goslineri* has black spots irregularly distributed over the entire body; *T. velox* has black lines and *T. inbiotica* red spots (Millen and Bertsch 2000). On the contrary, *T. goddardi* has an off-white background color, with various sizes and densities of brown spots, and it lacks black or red pigmentation. Also, the rhinophores, branchial leaves, extra-branchial and extra-rhinophoral processes, oral tentacles, and posterior end of the foot are the same color as the rest of the body, lacking yellow markings.

Internally, *Trapania goddardi* is easily distinguishable from the other eastern Pacific species of *Trapania*. The radula of *T. goddardi* is remarkably distinct by having an elongate and curved cusp situated on the outermost edge of the lateral teeth. *Trapania inbiotica* has denticles on the outer side of the cusp, a radular formula with 28 rows (Camacho and Ortea 2000), versus 17 in *T. goddardi*, and 21–24 inner denticles, many more than the 4–6 inner denticles of *T. goddardi*. *Trapania goslineri* has two outer denticles, a smaller one followed by a more elongate one; its radular formula is 37–41 and each tooth has 7–9 inner denticles. *Trapania velox* has a radular formula of 22–32 rows, with a long outer denticle and 8–11 inner denticles on each tooth (Millen and Bertsch 2000).

The reproductive system of *Trapania goddardi* is similar to the other species, except for *T. goslineri*, which has a semiserial bursa copulatrix (Millen and Bertsch 2000), whereas in *T. goddardi* it is serial.

There are two Indo-West Pacific species that have a white and brown coloration with patches: *Trapania brunnea* Rudman, 1987 and *Trapania safracornia* Fahey, 2004. The reproductive systems of *T. brunnea, T. safracornia* and *T. goddardi* are similar, but their external colorations are very different. *Trapania brunnea* has well-defined bright white blotches on a dark brown background (Rudman 1987). *Trapania safracornia* has a brown color with symmetrical white patches between the rhinophores, gill and posterior end of dorsum; the white patch on the gill area is saddle shaped (Fahey 2004) as opposed to the diamond shaped tan blotches of *T. goddardi*. The rhinophores of *T. brunnea* are brown in color with a white tip, slender and have a long tip that protrudes from the clavus; the rhinophores of *T. safracornia* are translucent with a red clavus and a white tip, whereas *T. goddardi* has stout rhinophores, off-white in color with brown specks. *Trapania brunnea* has white processes with a brown band, *T. safracornia* has yellow processes while *T. goddardi* has off-white processes with tan specks. The gill of *T. brunnea* is white with brown and red specks, the gill of *T. safracornia* is translucent with a pink tinge, and the gill of *T. goddardi* is off-white with brown blotches.

The radular teeth of *T. brunnea*, *T. safracornia*, and *T. goddardi* are similar, all having a long curved cusp situated on the outer edge of the lateral teeth. However, the number of primary and secondary denticles and size and shape of the large cusp are different in each species. The outer cusp of *T. goddardi* is proportionally longer compared to the width of the tooth than those of *T. safracornia* and *T. brunnea*. *Trapania safracornia* has 10–14 primary denticles per tooth with a smaller denticle between each pair of larger ones (Fahey 2004). *Trapania brunnea* has 15 denticles but the secondary denticles are not always present between the primary ones (Rudman 1987). *Trapania goddardi* has only 4–6 primary denticles which are considerably smaller than the outer cusp, and secondary denticles numbering up to three. The radular formula of the three species are 21 rows of teeth for *T. safracornia*; 30 for *T. brunnea* and 17 for *T. goddardi*. The jaws of these three species differ as well. *Trapania brunnea* has two rows of curved rodlets with sharp tips; *T. safracornia* has two rows of straight sharp rodlets; and *T. goddardi* has one row of rodlets with a single cusp and a wide base.

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Two New Cardinalfish Species of the Genus *Apogon* from Easter Island

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Three species of *Apogon* have been reported from Easter Island, two of which are here described as new: *Apogon kauteamea* (formerly *A. coccineus*), small, translucent red, with VI first-dorsal spines, a free edge of skin near the anterior nasal opening, and two rows of scales between the lateral line and the base of the third dorsal spine; and *Apogon rubrifuscus* (formerly talboti), distinct in having two predorsal bones and 12 pectoral-fin rays. It is similar to *A. deetsie* and *A. caudicinctus*, but has a much larger membranous preopercular flap, lacks any dark bars on the body, and attains larger size (101.5 mm SL).

Only three cardinalfish species have been recorded from Easter Island, *Apogon coccineus* Rüppell, *Apogon talboti* Smith, and *Apogon chalcius* Fraser and Randall (Fraser and Randall 1986; DiSalvo et al. 1988). Two, however, represented misidentifications. When Gon and Randall (2003) restricted *A. coccineus* to the Indian Ocean, the status of that species at Easter Island needed to be reevaluated. In 1986, Randall et al. collected a large (101.5 mm SL) *Apogon* specimen from a cave at a depth of 39.9 m that was reported by DiSalvo et al. (1988) as *A. talboti*. A closer examination of that specimen showed that it is not *A. talboti*. Both of these species were determined to be undescribed and are described here.

Materials and Methods

All counts and measurements follow Hubbs and Lagler (1964) except that the last two fin rays of the dorsal and anal fins are not counted as one unless it is clear that they are joined at the base. Measurements were made to the nearest 0.1 mm using dial calipers and are expressed as percentage of standard length (SL) or in relation to each other. Data for the holotype are presented first, followed by values for all specimens in parentheses. Ranges given in the descriptions are followed by the mean for measurements or mode for counts. Length of dorsal-fin spines was measured by placing one end of the caliper tip at the base of the spine pushed against the posterior base of anterior spine and the other caliper tip at the spine tip. Gill-raker counts include rudiments. Because *A. rubrifuscus* appears to be most similar to *A. deetsie* Randall (1998), and *A. kautamea* relates to the two complexes described by Greenfield (2001), the format for the description of each follows the format of each paper respectively to ease comparison. Institutional abbreviations are as listed in Leviton et al. (1985).

Species Descriptions

***Apogon kautamea* Greenfield and Randall, sp. nov.**
(Figs. 1–2; Tables 1–2)

Apogon coccineus (non Rüppell) Randall and Egaña, 1984.

Material Examined.— Holotype: CAS 219899, 40.3 mm SL. Easter Island, west coast off Tahai, 18–20 m, 13 February 1985, rotenone, J.E. Randall, A. Cea Egaña, and L.H. Di Salvo. Paratypes: BPBM 39186 (2, 33.3–39.2 mm), taken with holotype; CAS 219900 (3, 38.5–42.4 mm) Easter Island, off Motu Tautara, cave at 39.3 m, 10 February 1986, rotenone, J.E. Randall, A. Cea Egaña, L.H. Di Salvo, J.L. Earle, and M. Garcia; BMNH 2004.6.18.1 (1, 36.9 mm) Easter Island, west shore, wreck about 20 m offshore between Hanga Roa and Hanga Piko, 3.0–4.6 m, 27 January 1969, Chemfish, J.E. Randall and G.R. Allen; USNM 378013 (1, 37.9 mm) Easter Island, between Motu Tautara and Ara O Hara, cave with sand bottom, 16.8 m, 15 February 1985, J.E. Randall and A. Cea Egaña; FMNH 113713 (1, 39.8 mm) Easter Island, west coast, Tahai, large coral head on sand, 10.7 m, 18 February 1986, rotenone, J. E. Randall and M. Garcia ; AMS I.4330-001 (1, 40.8 mm) same locality as FMNH 113713; NSMT-P 68772 (1, 40.5 mm) same locality as CAS 219900; SAIAB (RUSI) 74299 (1, 39.8 mm) same locality as CAS 219900; BPBM 6634 (1, 25.4 mm), Easter Island, west coast, tidepools between Hanga Roa and Hanga Piko, 0.3–0.9 m, 25 January 1969, rotenone, G.R. Allen and B.A. Baker; BPBM 6635 (1, 41.3 mm), Easter Island, off Ahu akapu, 24.4 m, 5 February 1969 (color photo), J.E. Randall and G. A. Allen. *Apogon kuatamea*-non-type material: BPBM 6632 (4, 20.0–44.0 mm) Easter Island, off Ahu Akapu, rock and sand, 10.7 m, 7 February 1969, rotenone, J.E. Randall, G.R. Allen and B.A. Baker. *Apogon campbelli*: Pitcairn, BPBM 16927(2); Oeno Atoll (Pitcairn Islands), BPBM 16499 (2), BPBM 16533 (4); Tuamotu Arch., Mangareva Group, Temoe Atoll, BPBM 13529 (2); Rangiroa Atoll, BPBM 10310 (5); Society Islands, Tahiti, BPBM 10286 (3), Moorea, BPBM 6170 (1); Rapa: BPBM 39423 (3); Cook Islands, Rarotonga, BPBM 13946 (3); Aitultaki, BPBM 5613 (5). *Apogon crassiceps*. Holotype, Fiji, Viti Levu, MC 28214, BPBM 5795 (25), BPBM 38996 (1), CAS 218904 (12); Tonga, BPBM 38241 (2).

Diagnosis.— A small, usually less than 40 mm SL, semitranslucent, red species lacking stripes or bars or black edges on scales on body sides, with six spines in the first and one spine and 8–9 (almost always 9) rays in the dorsal fin; two spines and eight rays in the anal fin; usually a total of 16 or fewer gillrakers (rudiments included) on the first gill arch; 13–15 (almost always 14) pectoral-fin rays; two predorsal (supraneural) bones; a free edge of skin near the anterior nasal opening (Fig. 1F in Greenfield 2001); and two scales between the lateral line and the base of the third spine of the first dorsal fin.

Description.— Dorsal-fin elements VI-I,8 (VI-I,8-9, almost always I,9); anal-fin elements II,8 (II,8); all dorsal and anal soft rays branched, the last to base; pectoral-fin rays 14 (13–15, usually 14), the upper two and lower one unbranched; pelvic rays I,5; lateral line complete, the pored scales 24 (often plus one or two on caudal-fin base); predorsal scales 6; scales above lateral line to origin of first dorsal fin two; transverse scales 10 (9–10, usually 10); circumpeduncular scales 12; gill rakers 3 + 13 (3–4 + 12–14, usually 3 + 12 or 13), in holotype one developed on upper arch and 8 developed on lower arch, the remainder knobs.

Measurements based on holotype and 12 paratypes. Measurement for holotype presented first, followed by range for all types and the mean in parentheses all in percentage of SL. Counts based on 13 types plus three non-type specimens. Standard length 33.3–42.4 mm. Greatest body depth 36.7 (30.6–37.9: 35.6). Head length 39.0 (37.6–43.1: 39.5). Eye diameter 15.2 (13.4–15.8: 14.8).

FIGURE 1. Holotype of *Apogon kautamea*, CAS 219899.

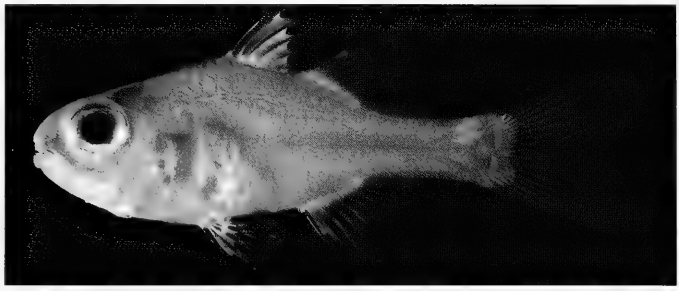

FIGURE 2. Fresh color of paratype of *Apogon kautamea*, BPBM 6635.

Snout length 7.3 (5.8–8.7: 7.2). Bony interorbital width 9.3 (8.1–9.4: 8.9). Upper jaw length 20.4 (19.7–21.8: 20.7). Caudal peduncle depth 13.7 (11.5–14.2: 13.1). Caudal peduncle length 31.3 (27.9–31.8: 30.2). First dorsal-fin base length 15.9 (15.0–17.5: 15.9). Second dorsal-fin base length 15.2 (14.1–15.9: 14.7). Anal-fin base length 16.1 (13.2–16.3: 15.2). Pectoral-fin length 24.8 (23.7–29.7: 26.6). Pelvic-fin length 26.8 (23.6–28.8: 26.0). First dorsal-fin spine length 5.0 (4.8–7.6: 5.9). Second dorsal-fin spine length 22.9 (21.6–24.1: 22.8). Third dorsal-fin spine length 17.7 (17.5–20.3: 18.9). Fourth dorsal-fin spine length 14.5 (14.2–16.6: 15.3). Fifth dorsal-fin spine length 10.2 (9.4–11.7: 10.6). Sixth dorsal-fin spine length 5.2 (4.7–7.0: 5.9). Length spine of second dorsal fin 14.1 (13.2–14.8: 14.0). Longest dorsal ray (1–3, usually 3rd) 21.9 (21.4–24.0: 22.5). First anal-fin spine length 4.6 (3.6–4.9: 4.2). Second anal-fin spine length 12.9 (11.8–13.2: 12.8). Longest anal ray (1–3, usually 2nd) 21.1 (18.9–23.9: 22.1). Upper caudal-fin lobe length 32.5 (32.1–35.8: 34.3). Lower caudal-fin lobe length 29.1 (29.1–39.2: 32.8).

Color of fresh specimen (from 35mm transparency of BPBM 6635). Head and body translucent, overlaid with a wash of red that is more concentrated on anterior and dorsal portions of body. Scales on nape strongly outlined in red and black pigment on predorsal scales. Scales on upper half of body outlined in red with a concentration of red along both dorsal-fin bases. Snout and side of head washed in light red, ventral surface of head white. Black area where brain is located showing through body. Back-bone showing through body as a red line, hypural plates also red. Red along anal-fin base. Dorsal and ventral edges of caudal peduncle with a concentration of red. Iris of eye gold, pupil black. Dorsal-fin spines and rays reddish, membranes clear. Rays of other fins with reddish tinge, membranes clear.

Color in alcohol: Head and body straw colored. Area over brain brown. Predorsal scales and scales along base of first dorsal fin with brown pigment. Scales on dorsal surface of caudal peduncle with scattered brown pigment spots. A few scattered brown pigment spots on scales at caudal-fin base. Iris of eye black, pupil dark straw. All fins clear.

ETYMOLOGY.— The specific epithet is a compound adjective from the Old Rapanui language of Easter Island, combining '*ku'ata*' meaning transparent and *mea* meaning red, referring to the transparent red coloration of the species.

COMPARISONS.— The distinctive nasal flap places *A. kautamea* in the *Apogon coccineus* complex; however, it has two scales between the lateral line and the dorsal-fin base that is typical of the *Apogon erythrinus* complex as defined by Greenfield (2001). The nasal flap is more complex than adding an additional scale row, and thus we consider *A. kautamea* to belong to the *Apogon*

coccineus complex. Two other members of the *A. coccineus* complex are known from the Pacific Ocean, *A. campbelli* and *A. crassiceps*. Both of these species have a single scale row between the lateral line and the dorsal-fin base. These two species are morphologically very similar, but differ in the number of pectoral-fin rays and gill rakers (Tables 1 and 2). *Apogon campbelli* appears to be an antitropical species, whereas *A. crassiceps* is more tropical. *Apogon kautamea* is morphologically similar to both species, and has counts similar to *A. campbelli*, but differs from both by having the unique combination of a nasal flap and two scales between the lateral line and dorsal-fin base.

TABLE 1. Gill-raker counts from both sides of species of *Apogon*

	Upper limb		*Lower limb*			*Total rakers*			
	3	*4*	*12*	*13*	*14*	*15*	*16*	*17*	*18*
A. campbelli	24	9	21	2	—	17	13	3	—
A. crassiceps	8	18	7	16	3	5	7	11	3
A. kautamea	30	2	15	14	3	15	13	3	1

TABLE 2. Pectoral-fin ray counts of species of *Apogon*.

	12	*13*	*14*	*15*
A. campbelli	—	3	29	—
A. crassiceps	1	25	—	2
A. kautamea	—	1	28	—

REMARKS.— With the discovery of *A. kautamea*, it is necessary to modify the definition of the *A. coccineus* complex as defined by Greenfield (2001). The single remaining character defining the *A. coccineus* and *A. erythrinus* phenetic complexes is the structure of the snout below the anterior nostril.

Apogon rubrifuscus Greenfield and Randall, sp. nov.

(Figs. 3, 4B)

Apogon talboti (non Smith) DiSalvo et al., 1988.

MATERIAL EXAMINED.— Holotype: BPBM 39346, 101.5 mm SL. Easter Island off Motu Tautara, cave at 39 m. Taken with rotenone by J.E. Randall, A. Cea Egaña, L.H. Di Salvo, J.L. Earle, and M. Garcia. 10 February 1986. *Apogon caudicinctus*: BPBM 35192 (4), Ogasawara Archipelago; CAS 219830 (2), Fiji. *Apogon deetsie*: BPBM 13983 (1), Hawaii. *Apogon posterofasciatus*: CAS 219901(3), Fiji; CAS 219902 (1), Fiji.

Diagnosis.—Dorsal-fin elements VI-I,9; anal-fin elements II,8; pectoral-fin rays 12; lateral-line scales 24; predorsal scales 6; gill rakers 5 + 15; body depth 2.9 in SL; upper preopercular edge serrate, the corner and lower edge with a protruding, cresentric membranous lobe with a crenulated margin that almost reaches the edge of the sub and interopercles; preopercular ridge smooth; caudal fin forked with rounded lobes; color pinkish red anteriorly with posterior two thirds dusky gray with black scale edges.

DESCRIPTION.— Dorsal-fin elements VI-I,9; anal-fin elements II,8; all dorsal and anal soft rays branched, the last to base; pectoral-fin rays 12, the upper two and lower one unbranched; pelvic rays I,5; principal caudal rays 17, the upper and lower unbranched; procurrent caudal rays three upper and three lower; lateral line complete, the pored scales 24 (plus two smaller pored scales on caudal-fin base); predorsal scales 6; scales above lateral line to origin of first dorsal fin one; scales below lateral line to origin of anal fin 6; circumpedunclular scales 12; gill rakers 5 + 15, all developed; pseudobrancial filaments 14; branchiosteal rays 7; vertebrae 10 + 14; supraneural (predorsal) bones two.

Body depth 2.9 in SL; body moderately compressed 2.2 in depth; head length 2.4 in SL;; dorsal profile of head straight (except for rounded front of snout); snout length 5.2 in head; eye diameter 2.9 in head; interorbital width 5.5 in head; caudal peduncle depth 4.1 in head; caudal peduncle length 3.4 in SL. Mouth slightly inferior and relatively large, maxilla extending to between the

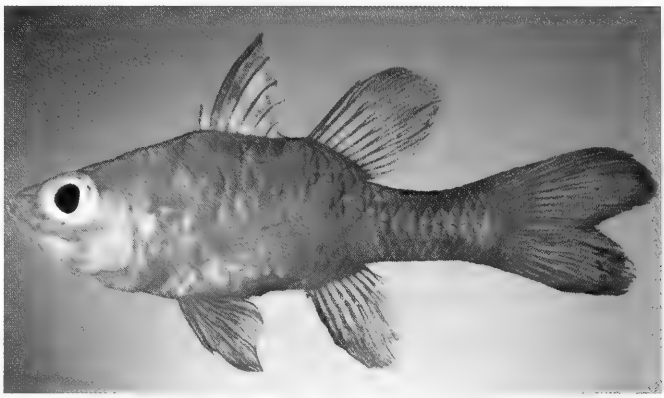

FIGURE 3. Fresh color of holotype of *Apogon rubifuscus*, BPBM 39346.

posterior pupil margin and posterior orbit edge; upper jaw length 2.0 in head; mouth slightly oblique, the gape forming an angle of about 40° to horizontal axis of body; supramaxilla not present; a band of villiform teeth in jaws (maximum of about 12 rows in upper jaw and five in lower jaw); a single row of about 17 very small, conical teeth on palatine; small conical teeth forming a V-shaped patch on vomer, two rows anteriorly and two rows posteriorly (vomerine teeth larger than those in jaws). Anterior part of tongue slender and spatulate. Largest gill raker at angle and adjacent to angle on lower limb, its length one-third eye diameter.

A single, acute, sharp, opercular spine at level of center of eye; upper edge of preopercle serrate, with 17 serrae; corner and ventral part of preopercular edge with a large, cresentric, protruding lobe with a crenulated margin that almost reaches edge of sub and interopercles and extends posterior of serrate edge; lateralis system of head with numerous close-set pores having slightly elevated rims; two longitudinal rows of pores from front of snout to occipit, crossed by 24 transverse rows; a suborbital row of pores with same transverse pore system. Anterior nostril a short membranous tube at level of bottom of pupil, about a nostril diameter from groove at base of upper lip; posterior nostril a larger triangular aperture, apex towards snout, directly in front of center of eye, the internarial distance about half pupil diameter; nasal chamber cavernous, the skin over the roof thin. Scales weakly ctenoid and thin; scales present on nape, opercle, and preopercle, those on opercle larger than scales on body; no scales on occiput, interorbital, snout, or ventrally on head; no scales on fins except for small scales on about basal fourth of caudal fin. Origin of first dorsal fin over third lateral-line scale; predorsal distance 2.4 in SL; fin spines strong and sharp; first dorsal spine 45.6 in head; second dorsal spine 2.1 in head; third dorsal spine slightly longest, 2.1 in head; second dorsal fin separated by two median scales (posteromost indented posteriorly) from first dorsal fin, its origin above ninth lateral-line scale; spine of second dorsal fin 2.3 in head; third soft dorsal ray longest, 1.5 in head; origin of anal fin slightly posterior to second dorsal-fin origin; first anal-fin spine short, 16.9 in head; second anal spine 2.5 in head; fourth soft ray longest, 1.8 in head; caudal fin forked with broadly rounded lobes; pectoral fins long and rounded, seventh ray longest, 3.0 in SL; pelvic fins reach to second anal-fin spine, 1.6 in head.

FRESH COLOR.— Background color of head and anterior part of body pinkish red; scale edges from first dorsal fin back to caudal fin black, and background color of caudal peduncle gray, making the posterior two thirds of the body much darker than the anterior third. Lateral-line scales on caudal peduncle paler than other scales, forming a distinct gray line down center of caudal peduncle sides. Preopercle and maxilla with silvery reflections. Pupil of eye black, iris silver. Spines and soft rays of dorsals, anal, caudal and pelvic fins pink to dark red, membranes dusky, so that the fins are dark. Pelvic-fin rays pink, membranes clear.

COLOR IN ALCOHOL.— Head and body straw yellow, with scale edges outlined in dark brown, particularly in posterior two thirds of body; fins pale except for outer edges of dorsals, anal, pelvics, and caudal fins; pectoral fins clear; iris of eye black with white pupil.

Etymology.— The specific epithet is a compound adjective from the Latin *ruber* (red) and *fuscus* (dark colored) in reference to the red body color overlaid by black pigment on the posterior two thirds of the body.

Comparisons.— Within the genus *Apogon* there are several species that have the same general body shape, one that is typical of *Apogon talboti* Smith. Because of this similarity, a number of specimens reside on museum shelves identified as *A. talboti*, but they are not. *Apogon talboti* has three predorsal bones and 13 pectoral-fin rays, whereas another group of specimens we refer to as "*talboti* look-alikes" have only two predorsal (supraneural) bones and 12 pectoral-fin rays. *Apogon rubrifuscus* belongs to this look-alike group.

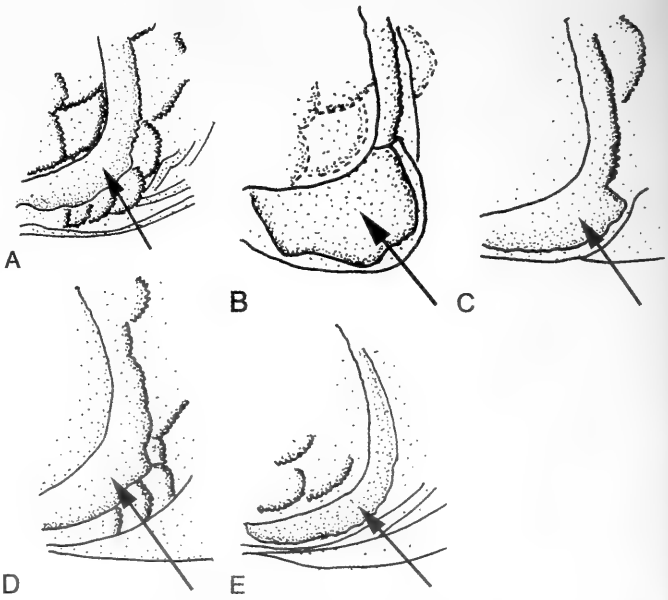

FIGURE 4. Preopercle and membranous flap indicated by arrow: (A) *Apogon talboti*, USNM 213228, Taiwan; (B) Holotype of *Apogon rubrifuscus*, BPBM 39346, Easter Island; (C) *Apogon deetsie*, BPBM 13983, Oahu, Hawaiian Islands; (D) *Apogon posterofasciatus*, CAS 219901, Fiji; (E) *Apogon caudicinctus*, BPBM 35192, Ogasawara Archipelago.

In addition to the three predorsal bones and 13 pectoral-fin rays, *A. talboti* has a distinctive, small, crenulated membranous flap at the lower corner and along the lower margin of the preoperculum (Fig. 4A). In their description of *A. posterofasciatus*, Allen and Randall (2002) state that it is most closely related to *A. deetsie* Randall (1998) and *A. caudicinctus* Randall and Smith (1988), and that "This trio is characterized by a membranous flap at the lower corner and along the ventral margin of the preopercle." Two of these species, *A. deetsie* and *A. caudicinctus*, have two predorsal bones, whereas *A. posteriofasciatus* has three. Ofer Gon (pers. commun. Oct. 2004) believes that *A. posteriofasciatus* is a member of the *A. talboti* group and not associated with *A. deetsie* or *A. caudicinctus*. *Apogon rubrifuscus* also has this membranous flap, and it is larger than that found in those three species (Fig. 4B). *Apogon rubrifuscus* and *A. deetsie* have a crenulated membranous flap below the suborbital bones, whereas it is smooth in *A. posterofasciatus* and *A. caudicinctus* (Fig. 4C–E). The preopercular margin of *A. caudicinctus* is more weakly serrate than in the other species, or smooth. The posterior end of the maxilla is concave in both *A. rubrifuscus* and *A. deetsie* whereas it is straight in both *A. posterofasciatus* and *A. caudicinctus*. *Apogon rubrifuscus* differs from *A. deetsie* by having more gill rakers (5 + 15 versus 3–4 + 12–13) and in coloration. *Apogon deetsie* has two dusky bars on the body, one below the basal half of the second dorsal fin and a broader bar posteriorly on the caudal peduncle and extending slightly onto the caudal-fin base. *Apogon rubrifuscus* lacks those bars, but rather has the entire caudal peduncle dusky as is a portion of the body anterior to the caudal peduncle. In preserved material, *A. rubrifuscus* has distinct dark scale margins whereas they are lacking in *A. deetsie*. Among the species considered here, *A. rubrifuscus* and *A. deetsie* appear to be most similar.

Key to the Easter Island Cardinalfishes

1a. Seven spines in first dorsal fin; overall life color golden yellow . . . . . *Apogon chalcius*
1b. Six spines in first dorsal fin; overall life color mainly red 2

2a. Corner and lower preopercular edge with protruding, crescentric membranous lobe with a crenulated margin that almost reaches edge of sub and interopercles; posterior two thirds of body dusky gray with black scale edges; five rakers on upper gill arch, all developed . . . . . *Apogon rubrifuscus*
2b. Corner and lower preopercular edge without large membranous lobe; body light without dark scale edges; three to four, usually 3 rakers on upper gill arch, only one developed . . . . . *Apogon kautamea*

Acknowledgments

The second author thanks foremost the National Geographic Society that funded his 1969 and 1985 fish visits to Easter island, and the Engelhard Foundation for its support in 1986. He is also grateful to Louis H. DiSalvo, Alfredo Cea Egaña, John L. Earle, and Henri and Michel Garcia for assistance in the field.

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Allenbatrachus meridionalis, a New Toadfish (Batrachoididae) from Madagascar and Reunion

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The third species in the genus *Allenbatrachus*, *A. meridionalis*, is described from Madagascar and Reunion, the southernmost occurrence of the genus. It differs from the other two described species, *A. grunniens* and *A. reticulatus*, by having more anal and dorsal-fin rays, differently shaped orbital cirri and maxillary barbels, and being darker in coloration.

The genus *Allenbatrachus* Greenfield previously included two species, *A. grunniens* (Linnaeus), known from India eastward to the Philippines, and *A. reticulatus* (Steindachner) known from Thailand south to Sumatra (Greenfield 1997, 1999). While examining specimens at the Muséum national d'histoire naturelle, Paris, the first author found several specimens from Madagascar and Reunion that represented an undescribed species of *Allenbatrachus*. Subsequently, the second author with colleagues from the American Museum of Natural History and Wildlife Conservation Society (WCS) collected three additional specimens of the same undescribed *Allenbatrachus* species from the Makira region of Madagascar. These specimens included a single specimen collected from a small freshwater stream just north of Ambodivoanongy, Sanavilory, and two specimens purchased from local fishers in the nearby Maroansetra market. The collection of these specimens confirms the previous report of Kiener (1963) who illustrated a toadfish specimen (identified in that publication as *Batrachoides grunniens*, now *A. grunniens*) from freshwater streams near the town of Maroansetra.

This undescribed species belongs to the genus *Allenbatrachus* because it has the following characters: (1) dorsocranium has a foramen on each side of the head behind the eyes, bordering the sphenotic and frontal bones (MNHN A3777 cleared and stained) (this character is shared only with species in the genera *Batrachoemoeus* and *Halophryne*); (2) it lacks the pore (foramen) present in the upper part of the pectoral-fin axil that is present in *Batrachomoeus* species; (3) the lower jaw is terminal, projecting beyond the upper jaw, whereas the upper and lower jaws are about equally terminal in *Halophryne* species; and (4) the interorbital width is equal to or less than the eye diameter and the gill slit is restricted to the upper one-half to two thirds of the pectoral-fin base in *Halophryne* species, whereas the interorbital width is greater than the eye diameter and the gill slit extends from the upper three-fourth to four-fifths of the pectoral-fin base in *Allenbatrachus*, the condition in the new species.

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Materials and Methods

All counts and measurements follow Hubbs and Lagler (1964) except that the last two fin rays are not counted as one unless it is clear that they are joined at the base. Measurements were made to the nearest 0.1 mm using dial calipers. All measurements are expressed as percentage of standard length (SL). Some counts were made with radiographs. Counts and measurements for the holotype are given first, followed by the range and mean or mode in parentheses for all specimens when variable. Institutional abbreviations are listed in Leviton et al. (1985).

Species Description

***Allenbatrachus meridionalis* Greenfield and Smith, sp. nov.**
(Figs. 1–6)

Material examinied.— Holotype: AMNH 233686, 147.2 mm SL, Malagasy Republic, Madagascar, Market at Maroantsetra, October 2003, P. V. Loiselle. Paratypes: CAS 220508, 169.0 mm SL, same locality as holotype. AMNH 234024, 90.7 mm SL, Malagasy Republic, Madagascar, small tributary of Antainambalana River, just north of Ambodivoanongy, Sanavilory, November 8, 2003, J.S. Sparks, W.L. Smith, K.L. Tang, and party. MNHN 1992-0670, 189.0 mm SL, Madagascar, Toliara, Tuléar, Andavadanova, 23°20′00″S; 43°30′0″E, Mauge. MNHN 1962-0197, 118.7 mm, 144.0 mm, 165.5 mm SL, Madagascar, Maroantsetra, Antainambalana estuary (listed as Antenambalana), Kiener. USNM 379463, 122.2 mm SL, same locality as MNHN 1962-0197.

Additional Material Examined.— *Allenbatrachus meridionalis* (non-types): MNHN A-3777, 109.6 mm SL, Reunion, 21°7′0″S; 55°35′0″E, cleared and stained. MNHN 1966-0912, about 180 mm and 194 mm SL, Madagascar, 20°0′0″S; 42°30′0″E, specimens bent, Kiener, Therezien. *Allenbatrachus grunniens:* Thailand: CAS 75217(2), CAS 75218(1). Vietnam: USNM 047986(1). Malaysia: AMS I.27634008(1). Borneo: CAS-SU 32944(2), CAS-SU 27732(4). Philippines: ANSP 48783(1), ANSP 77373(1), CAS-SU 26909 (1 cleared and stained), CAS-SU 38261(1), CAS-SU 38262(1), USNM 148493(1). India: CAS-SU 41321(1), AMS B.8319(1), ZSI 2099 (1 cleared and stained). *Allenbatrachus reticulatus*: Singapore: CAS-SU 30658(20, 1 cleared and stained), CAS-SU 33701(1), CAS-SU 35153(2), CAS 82188(1 neotype). Thailand: CAS 66821(1), CAS 75216(1), CAS 17652(1), CAS 88690(7), AMS I.21036003(2). Burma: ZSI 10741(1), ZSI 10957(1). Sumatra: USNM 333283(5).

Diagnosis.— A generally dark colored species of *Allenbatrachus* with 19 anal-fin rays, 22 dorsal-fin rays, usually a single, simple, pointed orbital cirrus, a simple, pointed barbel at the end of the maxilla, and pointed teeth.

Description.— Dorsal-fin elements III-22. Anal-fin rays 19. Pectoral-fin rays 21 (19-22, usually 19). Vertebrae 9 precaudal plus 19 (18-19) caudal (including terminal centrum). Upper lateral-line pores 27 (22-30, usually 27), lower lateral-line pores 18 (17-23), middle lateral-line pores, if present, indistinct. Head length 33.6 (33.1-39.9; 36.3). Head width 25.2 (25.2-31.6; 27.7). Head depth 16.6 (16.6-25.1; 20.0). Bony interorbital width 5.8 (4.8-7.2; 6.0). Fleshy interorbital width 9.8 (6.7-10.8; 10.1). Orbit diameter 5.4 (4.5-9.8; 6.2). Snout length 8.0 (5.9-9.2; 7.5). Upper jaw length 17.0 (17.0-18.6; 17.9). Width of mouth at rictus 17.9 (17.9-23.1; 20.2). First predorsal-fin distance 38.8 (38.7-41.7; 40.0). Second predorsal-fin distance 50.1 (50.1-54.7; 52.0). Preanal-fin distance 61.6 (58.5-64.2; 61.6). Prepelvic-fin distance 24.0 (21.2-26.8; 23.4). Greatest body depth 18.1 (18.1-28.4; 22.0). Caudal-peduncle depth 7.8 (6.5-8.8; 7.9). Length of second dorsal-fin base 43.5 (43.5-56.0; 49.4). Length of anal-fin base 33.1 (33.1-41.6; 37.7). Caudal-fin length 22.2 (20.4-24.0; 22.4). Pectoral-fin length 23.9 (22.9-28.7; 25.9). Pelvic-fin length 21.7 (19.7-23.8; 22.3).

FIGURE 1. Holotype of *Allenbatrachus meridionalis*, AMNH 233686.

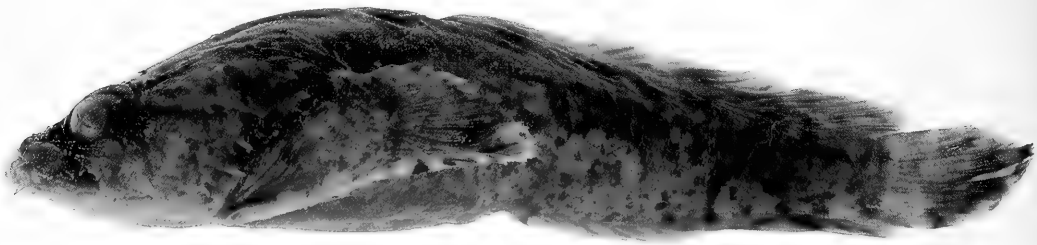

FIGURE 2. Paratype of *Allenbatrachus meridionalis*, AMNH 234024, from fresh water.

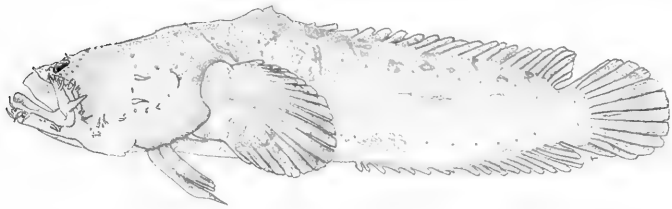

FIGURE 3. Drawing of paratype of *Allenbatrachus meridionalis*, MNHN 1992-0670.

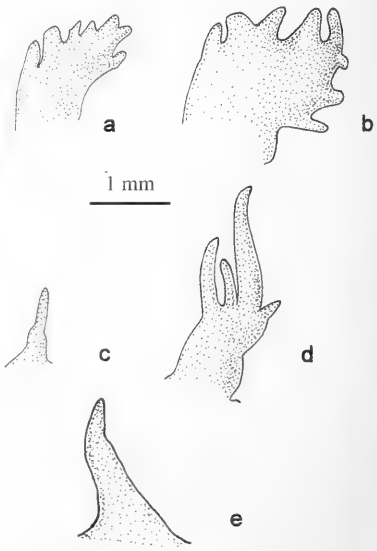

FIGURE 4. Orbital cirri. *Allenbatrachus reticulatus*: (a) anterior; (b) posterior. *Allenbatrachus grunniens*: (c) anterior; (d) posterior. *Allenbatrachus meridionalis*: (e) single cirrus.

Distance between pelvic-fin bases 6.1 (6.1-10.8; 8.6). A single, simple orbital cirrus, tip pointed (fig. 4e) (one specimen has three simple cirri on one side and two on the other, the central always the largest, and a second specimen had three on one side and one on the other with the central cirrus the largest; usually a single, simple orbital cirrus). Largest barbel at end of maxilla simple and pointed (Fig. 5c). All teeth in jaws pointed; vomer and palatines with a single row; dentary with single row on sides and triple row at symphysis; premaxilla with a double row on side and triple row at front.

Color in alcohol of holotype: Overall coloration of preserved specimens is dark, almost black, much darker than other species in the genus. Background color dark brown, with black color pattern. Sides of body

with irregular black blotches forming a band centered on the middle of the sides, the areas above and below this lighter. Ventral surface of head and body light brown, a distinct white area around the anus. Top and sides of head dark brown, overlaid with a heavy, irregular mottling of black. Pupil of eye white, iris black. Inside of mouth white. Pectoral-fin base dark brown with two black blotches, fin rays and membranes white, crossed by four distinct black bars, the distal margin of the fin white. Pelvic fin light brown, mottled with black blotches. Caudal fin light tan, covered with large, round black spots that form bars across fin, distal margin light tan. Second dorsal fin dark brown, with two black bands running the length of the fin, one along the base and the other along the distal margin, with a few brown tips on some of the membranes. Basal half of anal fin dark brown with black mottling, outer half a black band, white tips on the fin membranes.

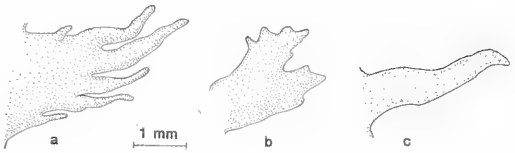

FIGURE 5. Largest barbel at end of maxilla: (a) *Allenbatrachus grunniens*; (b) *Allenbatrachus reticulatus*; (c) *Allenbatrachus meridionalis*.

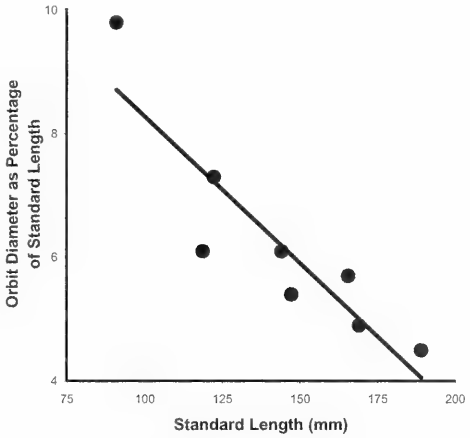

FIGURE 6. Orbit diameter as percent standard length versus standard length for *Allenbatrachus meridionalis* type specimens.

Color of fresh, small, freshwater specimen (AMNH 234024): Background color light tan with straw tinge, head and body overlaid with black markings. Head with black area in front of and under anterior half of eye, a black blotch behind eye with a line from it extending back across side of head. Another black blotch above eye and across interorbital area. Lower side of cheek, lower jaw, and underside of head cream. Area over opercle with black blotches running up across nape. Sides of body with irregular black blotches forming a band centered on the middle of the sides, wider on posterior quarter of body. Area below band light tan, with small, black spots. Pectoral fin light tan with black blotches forming indistinct bands, distal margin of fin white. Anal fin cream with some black blotches distally on posterior half. Base of caudal fin cream with black blotches on distal half. Distinct black blotch around base of first dorsal fin. Three black blotches along second dorsal-fin base. Second dorsal fin light tan with black mottling.

ETYMOLOGY.— The specific epithet is the Latin adjective *meridionalis*, meaning southern, referring to the fact that this is the southernmost known species of the genus.

COMPARISONS.— *Allenbatrachus meridionalis* differs from both other species of *Allenbatrachus*, *A. grunniens* and *A. reticulatus*, by having both orbital cirri and maxillary barbels that are simple and pointed rather than with multiple tips that are either rounded or pointed. It also differs from both by having more anal-fin rays, 19 versus 16–17. *Allenbatrachus meridionalis* has 22 dorsal-fin rays, whereas the other two species usually have 19. The new species is most similar to *A. grunniens* in having sharp, pointed teeth, rather than the rounded teeth found in *A. reticulatus*.

DISCUSSION.— The description of this species from Madagascar and Reunion considerably extends the range of the genus *Allenbatrachus*, previously known from the Ganges River area in India eastward to the Philippines. The capture of a specimen of *A. meridionalis* from a small fresh-

water stream as well as from saltwater habitats, concurs with the capture of the other two species in the genus in both fresh and salt water. The single, small (90.7 mm SL) freshwater specimen has a much larger eye than all other specimens, and at first we considered the possibility that it might be a different species from those taken in salt water; however, when orbit diameter as a percentage of SL was plotted against SL, it became evident that extreme allometric growth in eye size occurs in this species (Fig. 6). It also is lighter in color, with fin markings not as distinct as in larger specimens from saltwater habitats.

Acknowledgments

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The California Academy of Sciences Gulf of Guinea Expedition (2001) II. Additions and Corrections to Our Knowledge of the Endemic Amphibians of São Tomé and Príncipe

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We present observations on the São Tomé Island endemic *Hyperolius thomensis* which indicate that it is one of the few African treefrogs known to utilize phytotelmata (tree holes) for breeding. Our field work and observations strongly suggest that this island giant is restricted to primary forest, remnants of which are usually at higher elevations or inaccessible areas of São Tomé Island. Our locality data and field observations in a number of circumstances are not congruent with those of Loumont (1992). An examination of the data associated with her collections housed in the Natural History Museum of Geneva reveals that her data are not specific with regard to individual specimens and dates and, as a result, the status and distribution of the amphibian species on both islands may have been misinterpreted. We note that females of the endemic ranine ranid frog, *Ptychadena newtonii*, attain snout-vent lengths greater than other members of the genus, and that this species should therefore be considered an island giant. We describe and illustrate for the first time the males of Africa's largest treefrog, the Príncipe Island endemic *Leptopelis palmatus*, provide figures illustrating the range of male and female color pattern polymorphism and comment on adult size dimorphism and size at metamorphosis.

The islands of the Gulf of Guinea off the west coast of Africa are a unique chain that includes one geologically recent continental island, Bioko (formerly Fernando Poo), and three oceanic islands, Príncipe, São Tomé and Annobón (Pagalu). Isolated from the African mainland since their orogeny, the three oceanic islands are noted for their highly endemic but poorly known flora and fauna. In 2001, the California Academy of Sciences conducted a multidisciplinary, two-month research expedition to the two geologically oldest islands, Príncipe and São Tomé, which resulted in the collection of voucher specimens and tissues now available for genetic analysis. In an earlier study, Drewes and Wilkinson (2004) presented a more detailed introduction to the geologic history of the two islands, and a popular account of the expeditions' scope and goals is available (Drewes, 2002).

Loumont (1992) attempted the first comprehensive analysis of the entire endemic amphibian fauna of both islands. She recognized three hyperoliid species *Nesionixalus thomensis* endemic to São Tomé, *Leptopelis palmatus* found only on Príncipe, and *Nesionixalus molleri* common on both islands, two ranids, *Ptychadena newtoni* (São Tomé) and *Phrynobatrachus dispar* (common on both), and two species of dermophine caecilians, *Schistometopum thomense* and *S. ephele* of São Tomé. A subsequent morphological study (Nussbaum and Pfrender 1998) indicated that *S. ephele*

is conspecific with *S. thomense*, and we confirmed this decision based on mtDNA analysis (Stoelting, in prep.). In a recent systematic work, Drewes and Wilkinson (2004) returned *N. thomensis* and *N. molleri* to the genus *Hyperolius* Rapp 1842 from which these species were twice removed by Perret (1976, 1988; Loumont 1992).

Although the species that comprise the amphibian fauna of São Tomé and Príncipe have been known to science since the latter half of the 19th Century, these islands have rarely been visited by modern biologists and then usually only briefly. Thus, much of the natural history of these island species including basic data such as the extent of intra-island distributions has remained undocumented. We report data suggesting that the endemic treefrog *Hyperolius thomensis* of São Tomé is a primary forest, high-elevation, tree-hole breeding frog. We describe the male of the Príncipe endemic *Leptopelis palmatus* with comments on adult sexual size dimorphism and metamorph-adult size disparity. We attempt to refine our knowledge of the distributional limits of the amphibian species of São Tomé and Príncipe.

Materials and Methods

The CAS Gulf of Guinea expedition afforded the opportunity to examine localities on both islands in considerable detail and from the perspectives of five academic disciplines: herpetology, ichthyology, mammalogy, entomology and invertebrate zoology. Many sites on both islands were visited and sampled on multiple occasions. Three of the 11 CAS staff members involved in all or part of the 10-week expedition were herpetologists who spent roughly 110 person-days in the field. The availability of transportation and accessibility of many sites, especially on São Tomé, allowed us to conduct a reasonable amount of sampling and observation at night (until 2300 hr or later). All CAS specimens were hand-collected, euthanized, fixed in 10% buffered formalin and later transferred to 70% ethanol. Anuran larvae were retained in formalin. Tissues were taken from selected individuals of all taxa and preserved in 95% ethanol. Latitude, longitude and elevation were recorded with a Garmin 12 Global Positioning System receiver (datum WGS 84). All specimens and tissues are housed in the Department of Herpetology, California Academy of Sciences; associated data can be accessed on-line at *www.calacademy.org/research/herpetology/catalog*. Institutional abbreviations follow Leviton et al. (1985).

Results and Discussion

I. Reproduction in *Hyperolius thomensis*

In his initial description of the genus *Nesionixalus*, Perret (1976) found 25 large (2.0–2.5 mm) presumably ovarian eggs in each of two of the three females in the type series of *N. thomensis*. In erecting the genus, he suggested that the small number and large size of the eggs might indicate a specialized reproductive mode — "*un cycle biologique particulier*." Our field data suggest that Perret (1988) was correct. While our observations confirm that *H. molleri* deposits its egg masses above water in typical *Hyperolius* mode (Schiotz 1999; Fahr 1993; Figure 1 herein;), there is strong inference that *H. thomensis* is one of the few African tree-hole breeding frogs. To date, two bufonids, one microhylid, one petropedetine ranid, and five hyperoliids — *Acanthixalus spinosus, A. sonjae, Callixalus pictus* (possibly), *Hyperolius mosaicus* and *H. acutirostris* — are known to breed in phytotelmata (Rödel et al., *in press*).

In 10 weeks on São Tomé, we encountered *Hyperolius thomensis* at only two localities. A single, rather small male (CAS 219059; 31.0 mm.) was collected on 14 April 2001 among a group of *H. molleri* males, which were calling from tall grasses along a trail-side ditch on the footpath to Lagoa Amelia above Bom Successo (elevation: 1170+ m.). Our series of 13 adults (CAS

218925–937) was collected on 9 April 2001 within a hole in a buttressed, unidentified tree in primary forest at Macambrara, just west of the site of a large transmission tower at an elevation of 1280 m. This locality is a well-forested ridge top with no open water available. The tree hole was located where two buttresses were joined about 1.7–1.8 m. above the ground. The dimensions of the opening were roughly 7–12 cm wide by 25 cm high. The internal diameter of the hole was about 20 cm, and about 20 cm of stagnant water was in the basin. Two smaller holes were located on the same tree at least 1.7 m above the ground, one of which contained water and egg masses (but no adults); the other was dry.

When initially discovered on 9 April 2001, the first referenced tree hole yielded 11 adult *H. thomensis* — two adult females and nine males, 38 larvae and at least three egg masses adhering to the interior walls of the hole a few centimeters above the water surface. A subsequent visit to the tree on 16 April 2001 resulted in the collection of two more adult males. Of the two females collected, CAS 218925 has ovarian eggs whereas CAS 218934 has none.

We have not attempted to dismantle the egg masses, but each contains from 20–40 large, pigmented eggs. In one mass, the eggs are at the 32-cell stage of development (Gosner 1960, stage 7), and in another the eggs are at yolk plug stage (Gosner stage 11).

The 38 larvae range from Gosner stages 25–41 with the majority around 25–37. A detailed description of the larvae of *Hyperolius thomensis,* along with *H. molleri, Phrynobatrachus dispar* and *Ptychadena newtoni* is in preparation (Drewes and Altig); the *H. thomensis* tadpole has a maximum tooth row formula of 2(2)/3, but a number of individuals lack the second upper row (LTRF 1/3; nomenclature of Altig 1970). Ecomorphogically the larvae most closely fit the exotrophic, lentic, arboreal type 5 of McDiarmid and Altig (1999).

The large number of adults found together along with the various developmental stages of the tadpoles and egg masses suggests that tree-holes are used by multiple individuals at different times; phytotelmata probably represent primary reproductive sites at higher elevations where free water is absent. We assume based on buttress structure and trunk morphologies that there were additional holes that were too high to be surveyed in this tree and in other nearby trees of similar size.

RES returned to the radio tower site with other CAS team members on successive nights from 5–8 May 2001. On 5 May, beginning around 1930 hr, she heard an estimated nine different males calling from about 4.5 m above ground at locations approximately 30–40 m apart. Three locations within the forest where frogs were heard were marked. On 6 May, she and three others returned to the marked spots at about 2130 hr and noted a distinct reduction in calling from the night before. On this second evening, the moon was full, and there was a lack of mist. At one marked spot she heard a male calling from the same perch as on the night before and noted that a few other males seemed to be calling from sites somewhat lower within the canopy than on the previous occasion. Individuals were extremely wary: if disturbed they ceased calling, and then seemed to resume from another spot. On the night of 7 May, numerous frogs were again heard from "all over the radio tower primary forest area [= Macambrara]," but no calls were heard along the road to the lower plantation areas. Finally, on the night of 8 May at around 1900 hr near the original tree from which the *H. thomensis* series was initially collected on 9 April, RES heard, recorded and saw a single individual about 7 m above ground at the juncture of a bifurcating tree trunk. The recording is consistent with the description and sonogram given in Loumont (1992). Upon descending to Bom Successo she noted that no calls were heard in cultivated areas, but a few were heard in a remnant of primary forest between the plantation and Bom Successo.

Our extensive field work on São Tomé leads us to the conclusion that *H. thomensis* is a high-elevation, primary forest, tree-hole breeding species, which is not consistent with collecting localities given in Loumont (1992).

II. Localities and Distributions

We were puzzled by our inability to confirm some of the *H. thomensis* localities cited in Loumont's paper and by the absence of supporting data that one would normally expect to see (e.g., specific collecting dates, voucher numbers associated with sonograms, and behavioral observations). Published sonograms of male advertisement calls by *H. thomensis* that were supposedly collected at Java and Colonia Açoreana indicate that they were recorded from captive males calling in plastic bags (as were the recordings of *Phrynobatrachus dispar* and *H. molleri* [Loumont, p. 40]). However, there are no individual voucher numbers provided with these sonograms, and it is not clear from which specimens these calls were recorded, nor where they were made — on-site, in the town of São Tomé or in Geneva. Although the sonogram of *H. thomensis* is accurate based on our recordings and observations noted above, we assume that Loumont failed to note calling sites, times and specific dates because she did not collect nor observe these specimens in the field. Additional inconsistencies lead us to believe that much of her hyperoliid material was brought to her by local collectors.

Loumont indicated that specimens of *H. thomensis* were found in São Tomé town (coastal), Colonia Açoreana (coastal), Java (600 m), and Monte Café (680 m) under banana leaves, and in mossy hollows in old walls, close to small reservoirs of water; these represent the entirety of the microhabitat information provided by Loumont (*op. cit.*, p. 51) for this species. We sampled the abandoned plantation at Java on several occasions but found no evidence of *H. thomensis*, although *H. molleri* adults, tadpoles and egg masses were readily found in such microhabitats. No suitable sites were found in the town of São Tomé in spite of many days of searching there and at many other coastal and lowland localities. We did not survey Monte Café (500+ m below the CAS Macambrara site), but in October-November 2003, a private collector camped for three days at Pousada Boa Vista while actively looking for *H. thomensis* and other endemics. Pousada Boa Vista is above Monte Café on the same road, ca. 800 m. Five *H. thomensis* were brought to him by a local boy who indicated they came from a site about an hour away and stated that they were "very hard to find." (Daniel Hofer, pers. commun.). The CAS expedition did not survey the coastal locality of Colonia Açoriana *per se* but worked many similar sites along the east and southeast coasts (Micondó, vicinity of Rio Angobó, Sao Joao, vicinity of Dona Augusta).

The Natural History Museum in Geneva kindly provided by electronic mail all of the field data associated with Loumont's collections of *H.* (as *Nesionixalus*) *thomensis* and also of *Leptopelis palmatus* (Príncipe Id.). Loumont's collection dates with respect to nearly all of these specimens are recorded inclusively rather than as individual dates. For instance, Loumont's data for 21 "*Nesionixalus*" *thomensis* contain but one specific date: 10.07.1988 for two specimens from Java. Two specimens from Monte Café bear the date 7.1988. Four more from Java are recorded as 1.1990, and the remaining specimens from São Tomé town, Gulf of Guinea, Monte Café, Agua Cascada, Colonia Açoreana and Java all bear the collection date 1.12.1989–31.12.1990, a 13-month period. The Agua Cascada specimen (MHNG 2492.084) and the two from "Golfe de Guinée (MHNG 2492.081–082) were not included in her publication, but the MHNG data sheets indicate the same collecting date as the others: 1.12.1989–31.12.1990. Similarly, all *Leptopelis palmatus* taken from three separate localities on Príncipe Island are cataloged as having been collected from 1.12.1989–31.1.1990. In her materials and methods section, Loumont (1992) stated that field work took place in early July 1988 and in January 1990. If this is accurate then any and all specimens taken during December of 1989 must have been collected by someone else prior to her arrival.

We conclude that Loumont did not publish nor archive individual collection dates or more specific locality site data because she did not know them, and that she relied on local collectors for

collection of the specimens and for their general locality data. Data such as "Golfe du Guinée" is consistent with the broad and technically correct information a researcher might record for a valuable specimen if more precise locality data was unknown or had been lost. Similarly suspect is the collection locality of Colonia Açoreana. Colonia Açoreana is a lowland site on the southeastern coast at about 200 m and surrounded by old plantations and secondary growth; however, the topography inland rises to above 600 m within 6 km of the town where primary growth likely still persists. We think it is reasonable that a local collector bringing specimens to São Tomé city would probably indicate "Colonia Açoreana" as the point of capture for animals that had perhaps been collected at an un-named locality high in the mountains above that town.

Loumont indicated that most of her localities were within two ecological zones on both islands: a lower altitude zone from 0–500 m, where *Ptychadena*, *Phrynobatrachus* and *Leptopelis* are found, and a middle montane zone (500–1000 m) where "*espéces parasylvicoles*" (species of disturbed-forest/secondary forest?) such as *Nesionixalus* (= *H. thomenis and H. molleri*) occur but they may also descend to the lower plains. She mentions three other zones from which she had no specimens: the northeast savannah on São Tomé (grassland with baobab trees [*Adansonia digitata*] in the rain shadow of Pico do São Tomé, the primary site of 16th Century sugar production by the Portuguese), the areas adjacent to the central peak (from 1500 to 2000 m), and the forests of middle elevation on the southern exposures of both islands which are inaccessible by road.

During our stay there, the local inhabitants and expatriates on São Tomé were consistent in telling us that amphibians were not found above 500 or 600 m, but Schiøtz (1999) wrote that *Hyperolius* (as *Nesionixalus*) *molleri* occurs between 500–1000 m, evidently following Loumont (1992). Below, we provide species distributions based on our own data for specimens collected at altitudinal extremes, our interpretation of Loumont's (1992) data and records by J. Baillie (1999).

Hyperolius thomensis Bocage, 1886. This frog is the largest member of the genus *Hyperolius* and an island giant. *H. thomensis* is an endemic to São Tomé Island and restricted to remnants of primary forest which are usually at higher elevations above 800 m. The five type specimens lost in the Lisbon fire included a male and female from Roça Saudade (800 m), a male and female from "Ile São Tomé" (exact provenance unknown), and a single female from the Rio Quiza (= Rio Quija, A. Gascoigne, pers. commun.), a river in the southwestern part of the island with headwaters at 900 m. Specific localities documented by voucher specimens include CAS 219059, above Bom Sucesso on trail to Lagoa Amelia (ca. 1170 m) and CAS 218925–218937, in the tree hole on primary-forested ridge at Macambrara (1280 m.). Probable localities (viz Loumont, 1992) are forest remnants on slopes above Monte Café and Java, and inland from Colonia Açoreana. We reject the capital city of São Tomé as a locality for this species. It is likely that this species still exists wherever primary forest remains, especially on the steep terrain of relatively inaccessible southern slopes of the island.

Hyperolius molleri Bedriaga, 1892. A common *Hyperolius* on both São Tomé and Príncipe islands, this species appears to be a classic "farmbush" species, *sensu* Schiøtz (1967). It breeds in still or very slow-moving water; egg masses are deposited on overhanging vegetation (Fig. 1). On São Tomé, *H. molleri* occurs at sites near sea level adjacent to São Tomé town such as at Praia Melão (CAS

FIGURE 1. Egg mass of *Hyperolius molleri*. São Tomé: Quisinda. Photograph by D. Lin

219068–219069), is common in both low and mid-elevation abandoned and functioning plantations such as those at Caxueira (CAS 218848–218891) and Java (218974–218994), and specimens were found calling from bushes on the banks of Lagoa Amelia in primary forest at 1412 m (CAS 219048–219050).

On Príncipe, *H. molleri* was found in the same microhabitats as on São Tomé. CAS 219203–219208 were collected while calling from vegetation near pooling areas of a small stream at sea level, just in from our campsite on the beach at Baia das Agulhas on the southwestern coast. Another series was taken at about 150 m near the town of Santo Antonio while males called from vegetation overhanging eddies of the slow-moving Ribeira Doutor. Notably, RES did not encounter *H. molleri* at higher elevations during her ascent of Pico do Príncipe.

Leptopelis palmatus (Peters, 1868). Endemic to Príncipe Island, this species has hitherto been considered a lowland treefrog based on three localities reported by Loumont (1992), who suggested it was found up to 300 m. CAS 219370–219383 and 219397–219401 were collected at about 620 m on the central massif of Pico do Príncipe; BMNH 2000.58 was taken at approximately 700 m during a daytime descent from Pico do Príncipe by Jonathan Baillie in 1999. (Baillie, personal communication) Because this collection is the basis for the first description of the male of this species, it is treated in further detail in Section III, below.

Ptychadena newtoni (Bocage,1886). This São Tomé endemic may be the only true lowland amphibian species *sensu* Loumont (1992); all of her collection localities are in the northern lowlands of São Tomé Island (north of a line between São Tomé town and Diogo Vaz on the northwest coast), well below 150 m. We collected two series of adults in town (CAS 219248–219263 in an undeveloped lot, and CAS 219313–219317 in a swampy area of Agua Grande). We also collected a series of *P. newtoni* tadpoles (CAS-RCD 13682) together with *Phrynobatrachus dispar* larvae in a road-side puddle at Java (595 m), which would constitute an altitude record for these species. At this site, no adults were seen. A description of the *P. newtoni* tadpole and others is in progress. *P. newtoni* is the only endemic amphibian species of São Tomé and Príncipe that may be endangered. Since Loumont's visit, many low-lying areas in the vicinity of São Tomé town have been drained for housing. We visited a number of sites at which we were told this species used to be common; in most cases, the areas were dry.

Loumont (1999) records a female *P. newtoni* of 76 mm, snout-vent length. To our knowledge this is the largest known *Ptychadena* specimen. This indicates that together with *Hyperolius thomensis*, and *Leptopelis palmatus*, there are three examples of anuran island gigantism inhabiting the Gulf of Guinea Islands.

Phrynobatrachus dispar (Peters, 1870). This species was originally described from Príncipe Island; a second species, *Phrynobatrachus feae* (Boulenger, 1906) also from Príncipe, was described later. The differences between descriptions are rather minor, and Loumont (1992) concluded that the latter is a synonym of the former. The CAS expedition took tissue samples from a number of populations on both islands but has not yet sequenced them. We treat these taxa as one, *Phrynobatrachus dispar*. *P. dispar* is a nearly ubiquitous frog in suitable wet areas in disturbed as well as near-pristine conditions on both islands. CAS 218918–218919 and 219064–219077 were collected at 700 m in aqueduct tunnels of the Rio Contador on the west side of São Tomé Island; CAS 219047 was taken from the edge of Lagoa Amelia at 1412 m. On Príncipe Island *P. dispar* was collected by RES at 620 m (CAS 219385–219393) in a tributary of the Ribeira Banzu, and on the top of Pico do Príncipe at 948 m (CAS 219393–219394). Baillie (1999) records the species as very common on the top of Pico Mesa, ca. 530 m.

Schistometopum thomense (Bocage,1873). The endemic São Tomé caecilian is perhaps the most unlikely amphibian inhabitant of the island from a dispersal point of view. Wholly fossorial,

it might be expected to occur principally in the lowlands, but such is not the case. Two specimens were collected on the west side of the island in a vertical rock crevice along the Rio Contador culvert at 700 m. (CAS 218914–218915), and a series (CAS 219324–219334) was found in a cultivated field above the arboretum at Bom Sucesso, ca 1180 m. J. Measey (personal communication) has collected specimens of *S. thomense* within 100 m of the Lagoa Amelia crater rim (which would be at about 1300 m).

III. The male of *Leptopelis palmatus*

Prior to the CAS Gulf of Guinea expedition, the Príncipe endemic treefrog *Leptopelis palmatus* (Peters, 1868) was represented in collections by the female holotype (ZMB 6067: "île de Principe"), eight females from three lower-elevation localities reported by Loumont (1992) and deposited in the MHNG, and two males and a female in the collections of BMNH collected by J. Baillie in 1999. Loumont (1992) published a table of measurements of the females including MHNG 2491.82 from Bela Vista with a snout-vent length of 110 mm, indicating that *Leptopelis palmatus* attains a greater snout-vent length than any other African treefrog species. She included a photograph of one of the females (1992, fig. 7; museum number not given) which illustrated the dorsal pattern described as marbled (*"un aspect marbré"*); she described the other specimens as being dark green or black with a number of light patches. A photograph by Loumont of what appears to be the same specimen is presented in Schiøtz (1999, fig. 570), which together with the aforementioned comprise the only published images of *L. palmatus* to date excepting three on-line images by Baillie (1999). Figure 2 illustrates the range of color pattern variation we observed in females. Figure 2A is a 108 mm SVL individual collected in at Tchipique, a locality in the northwestern part of Príncipe Island; Figure 2B is 88 mm SVL from the Rio Papagaio a central island locality. BMNH 2000.58, the smallest mature female known (oviducal eggs present) exhibits a dark brown pattern on a beige background which we interpret as cryptic.

Our series of eleven adult male *L. palmatus* was collected by the second author (RES) over 17–18 May 2002 on the massif of Pico do Príncipe along a tributary of the Ribeira Banzu at about 620 m elevation. The same locality yielded two females, three juveniles and three post-metamorphs (Appendix I). The locality is a small cascading stream in primary forest dominated by saplings and tree ferns (the endemic *Cyathea camerooniana* var. *currori*). The specimens were collected from 1800–0030 hr on the 17 May and 1800–2000 hr on 18 May. The males were perched on leaves or branches of saplings or leaves of tree ferns from 1.0–1.5 m above ground, although the larger

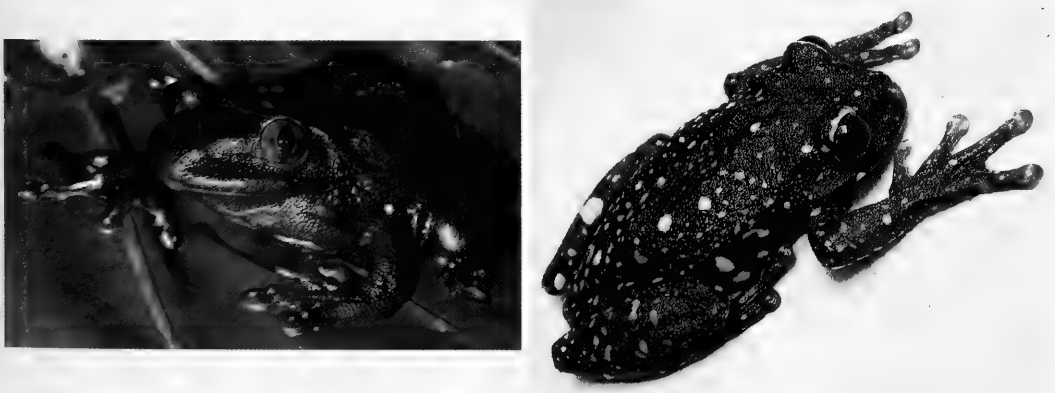

FIGURE 2. (A) CAS 219177, female *Leptopelis palmatus*. Príncipe: Tchipique, near Sundi. Photograph by D. Lin; (B) CAS 219351, female *L. palmatus*. Príncipe: Rio Papagaio. Photograph by J. Ledford.

female (CAS 219401) was found on the ground beneath a rocky overhang near a pool at the base of a small waterfall. A small post-metamorph, CAS 219370, was found perched on the same leaf as an adult male. RES collected an area about 10 m out from both banks of the stream along approximately 30 m of its length and found the tree frogs remarkably numerous: she saw three times as many specimens as she collected (ca. 60 seen). On both nights RES heard calls of *Phrynobatrachus dispar* which were numerous in the leaf litter near the stream, but did not hear any advertisement call attributable to *L. palmatus* males.

Description of males

Adult male *Leptopelis palmatus* specimens are less than half the snout-vent length of females (male mean = 41.4 mm — Appendix I; female mean = 93.8 mm, n = 12, including data from Loumont, 1992). *L. palmatus* males are remarkably polymorphic for color pattern; male color patterns include individuals with uniform bright green dorsum, slightly darker green with random mustard blotches or faint blackish vermiculations, pinkish maroon with indistinct olive blotches and occasional dull-orange spots, mottled light brown and white, and light brown individuals with fairly distinct partial "X"-shaped patterns on the dorsum and distinct thigh bands. (Fig. 3). The dorsal and lateral skin of all specimens is heterogeneous and rough, as in females. The male ventrum is not dark as in females, but ranges from off-white to lightly mottled gray.

In larger females, there is a conspicuous fold of skin extending across the head between the posterior margins of the tympani. This structure is quite obvious in Peters' drawing of the holotype (1868), in Loumont's photographs (1992, in Schiøtz 1999) and in our own Figure 2A. This feature was not discussed in Perret's examination of the type (1973). It is absent in all male specimens and also absent in smaller CAS females (219351; 219401) photographed in life.

The irises of all males (and females) are a deep ruby-red in life, in contrast to the gold iris of *L. rufus* (Schiøtz, 1999) with which *L. palmatus* was compared in an earlier study by Perret (1973) (Figs. 2–3). This ruby iris color is most similar both in hue and extent to that of live specimens of *Leptopelis parkeri* of East Africa. As suggested by the figures in Schiøtz (1999), whereas many species of *Leptopelis* have reddish coloration in the dorsal quarter to fifth of the iris, only a few appear to consistently have red irises, and these are of a lighter shade than *L. palmatus*, e.g. *L. kivuensis* and Nigerian *L. boulengeri*.

The tympanum in males is conspicuous and measures a little less than one-half the diameter of the eye as in the female (Perret 1973). The eyes are large and protruding, their horizontal diameter nearly equal to the interorbital distance.

The toes of the males are nearly as fully webbed as in females, but the proximal side of the terminal phalanx of toe IV is free. The fingers of males are less webbed than those of the females; the area between toes IV and III is about one-half webbed, that between III and II about one-quarter webbed (for comparison, see figure of holotype in Boulenger [1882:136]). Males possess poorly defined pectoral glands discernible as light patches posterior to the posterior edge of the insertion of the forelimbs.

Dissection of the gular regions of three males (CAS 219373; 219377 and 219400) revealed that *L. palmatus* males lack a vocal sac; there is no elaboration of the *m. interhyoideus*. Vocal sac openings are absent. This is a unique condition within the genus *Leptopelis* although there have been few studies that include these characters (e.g., Drewes 1984, for 11 species).

Male advertisement call

The advertisement call of male *L. palmatus* has never been recorded nor analyzed; however,

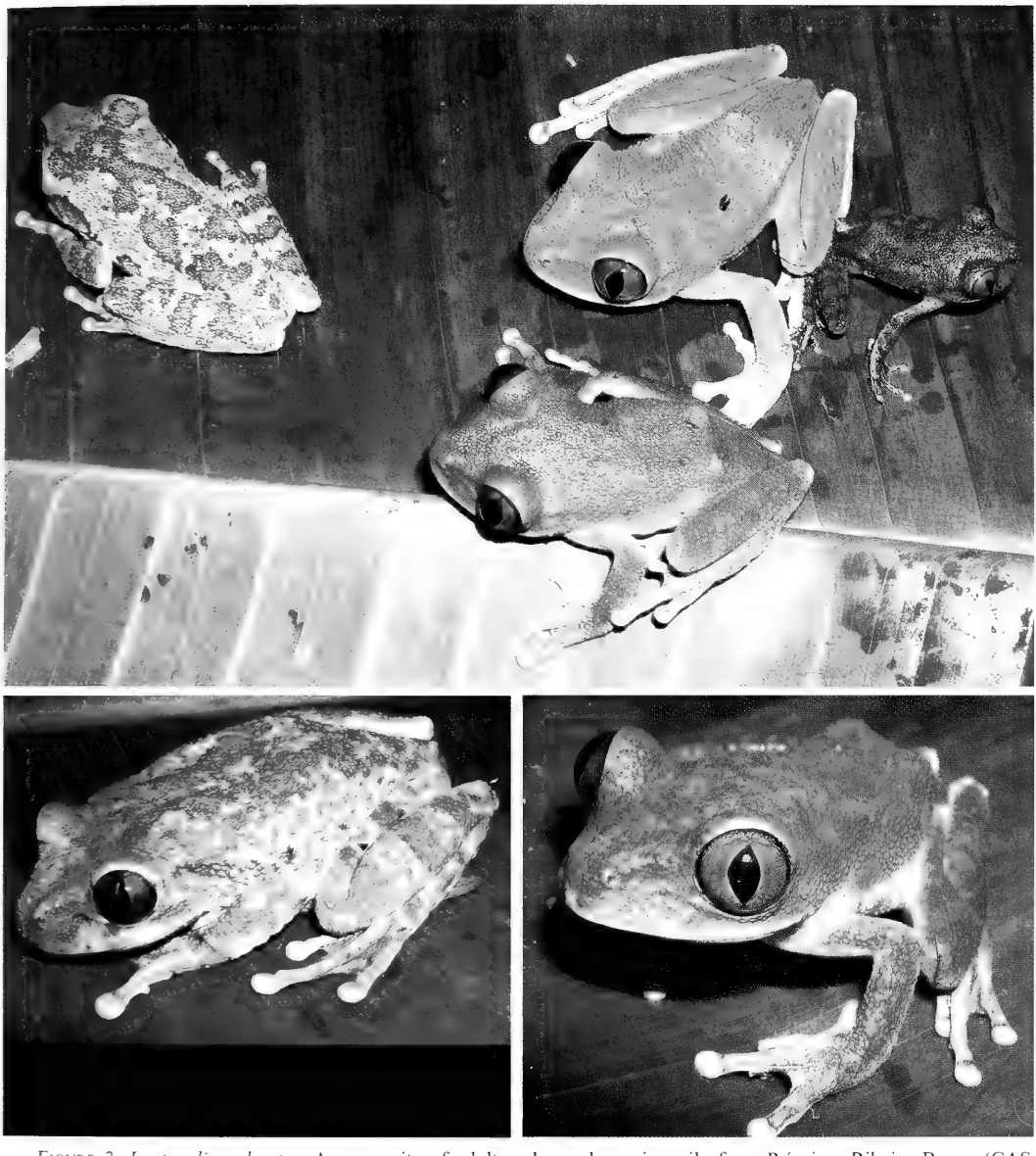

FIGURE 3. *Leptopelis palmatus*. A composite of adult males and one juvenile from Príncipe: Ribeiro Banzu (CAS 219371–219383, 219400). Photographs by J. Ledford.

we were assured by the local inhabitants of Príncipe Island that males do call, and the presence of well-developed tympani in both males and females tends to confirm the fact. On the evenings of 5/17 and 5/18, REL heard multiple calls of *Phrynobatrachus dispar* but no calls referable to *Leptopelis*. Males did not call in captivity during transfer back to Santo Antonio. In 1999, the male call was described by Jonathan Baillie in his on-line account of his dissertation field research on Príncipe Island. The following is an excerpt from his account dated 1 September 1999:

> In the dark we took flashlights and cameras to try and find the frogs responsible for the loud night chorus. *Phrynobatrachus dispar* was also common in the small streams. . . . If you listen closely you can hear the soft repetitive peep-peep-peep of this tiny frog. The more noticeable croaking noise, more like a pop bottle being continuously opened, belongs to the tree frog (*Leptopelis palmatus*) that is found in high densities (we saw about 50 that night) on the branches and vines in close proximity to the stream.

This "popping" sound had been described to us by locals earlier in Príncipe's only town, Santo Antonio, and it is consistent with the non-resonant call that might be associated with males lacking a vocal sac. If this call is correctly assigned, it is very different from the call described onomatopoetically by Schiøtz (1999:256) for *Leptopelis rufus*: "a series — about ten long cries [of] 'yiin.'" Baillie's account and personal communications suggest that the campsite near which these observations were made was probably the same site at which RES collected the CAS series of *L. palmatus,* or at least very close to it (Baillie's local guide, Monauna, a former parrot hunter, also guided the CAS party nearly two years later). On 5 Sept, Baillie again heard *L. palmatus* advertisement calls at about 700 m in the forest of Morro de Leste, a ridge approximately 3 km ENE of Pico do Príncipe, but could not locate any individual frogs (Baillie 1999).

Island effects

Female *Leptopelis palmatus* are both the largest of that hyperoliid genus and the largest known African treefrog. They are also among the few anuran island giants that have mainland congeners including *Hyla vasta* and *Eleutherodactylus inoptatus*, both of Hispaniola (Cochran 1941; Zug et al. 2001). The two islands of São Tomé and Príncipe have a number of endemics that are classic examples of island gigantism (Carlquist 1965). On São Tomé, some of these include the largest treefrog of the hyperoliid genus *Hyperolius* (*H. thomensis,* Drewes and Wilkinson 2004), the largest member of the widespread African ranid genus *Ptychadena*, *P. newtoni,* the largest nectariniid sunbird, *Dreptes thomenis* (Cheke and Mann 2001), and the giant two-meter begonia, *B. baccata* (Plana et al., 2004). Both islands share the endemic gecko, *Hemidactylus greefiii*, which is the largest African member of that genus (Loveridge 1947). Although it is an obvious and frequently documented phenomenon, island gigantism is not well understood; release from competition for resources and predation have been suggested as causative factors.

Our series of male *Leptopelis palmatus* exhibit what appears to be non-fixed color pattern polymorphism. Some non-cryptic, arboreal African treefrogs, notably populations of the *Hyperolius viridiflavus* complex, exhibit striking inter- and intrapopulational variation in color pattern, which has led to a proliferation of taxonomic names (Schiøtz 1971). Within such populations, this variation can usually be assigned to one of a number of phases. For instance, Schiøtz (1967), described in *Hyperolius* a PhJ or juvenile phase exhibited by all juveniles and some adult males and a PhF, the female phase, exhibited by all adult females and some males. In our series of male *L. palmatus*, color and pattern are seemingly random, and there appears to be no selection for crypsis (Fig. 3). We know of no other African treefrog with this magnitude of color pattern variation. Females are dull green, brown or black, whether marbled or not (Figs. 2A–B). We considered the possibility of a sexual difference in microhabitat which might account for the less variable, more subdued coloration in females. Although all of the CAS males were collected in arboreal situations, two of the CAS females, 219177, the largest, most heavy-bodied specimen (Fig. 2A), and CAS 219401 were found — at different localities — on the ground in moist areas protected by overhangs (Appendix, Table 1). BMNH 2000.58 was found on the forest floor. The other two females, CAS 219399 and 219351, were collected while perched. Unfortunately, our sample of females is

limited to five as there are no habitat data associated with the eight females Loumont deposited in Geneva (MHNG).

Sexual size dimorphism is the rule among *Leptopelis* species, and, based on specimens collected. *L. palmatus* exhibits the greatest disparity between adult male and female snout-vent lengths of any species of the genus. Schiøtz (1999) provides male and female snout-vent maxima for 33 of the 44 species of *Leptopelis* he recognized and in most species, males range from 8–20 mm smaller in snout-vent length than females. Table 2 (see Appendix) is a compilation of maximum male and female snout-vent lengths recorded from the seven *Leptopelis* species in which the females are greater than 20 mm in length than the males. Our data indicate that the largest known *L. palmatus* male is only 41% of the snout-vent length of the largest female. Mean male size is 45% of mean female SVL. The only other species in which males are less than half as long as females is the widespread West African mainland species, *L. macrotis* at 45% (based on SVL maxima). In addition, we are unaware of any other anuran species that exhibits such as marked range of SVL among adult females (Appendix I).

There is a full order of magnitude difference in *L. palmatus* between post-metamorphic size (10.5–11.3 mm, Gosner stages 45, 46 — Table 2 in Appendix) and potential adult size (MHNG female 2491.82–110 mm; Loumont 1992). Nothing is known of the breeding biology of *L. palmatus*, and the larvae have yet to be discovered. Small size at metamorphosis can be interpreted as an indication that the water in which early development takes place is ephemeral (this would seem unlikely on Príncipe which has high rainfall especially in the forested higher elevations) or that predation on developing larvae is high. Baillie (1999) noted abundant crabs of about 9 cm in diameter feeding in the river at night at the same elevation (and presumably at the same *L. palmatus* collection site; see above), and these may be a significant predator on small frogs. CAS 219370 (11.0 mm) was perched on the same leaf as an adult *L. palmatus* male (field number not noted), about 1.5 m above ground, suggesting both resource availability for individuals at both sizes and perhaps avoidance of predation by crabs. However, RES observed no crabs during her visit to the site. The CAS *Leptopelis palmatus* were removed and taken to lower elevation for photography, processing and removal of tissue; as a result an examination of stomach contents was not informative.

Reduction of predation pressure may well be a factor in the extreme variation in color and pattern observed among *L. palmatus* males (at least for the known sample which was collected at densely-forested higher elevations). Color pattern variation appears much reduced in females suggesting that females are under a different selection regime.

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Appendix

TABLE 1. *Leptopelis palmatus* specimens collected on Príncipe Island by the CAS Gulf of Guinea Expedition including three specimens from the BMNH. Sexual maturity was determined by dissection in male specimens greater than 33 mm SVL.

Sex	*Museum*	*Catalog number*	*Locality*	*Snout-vent length (mm)*
Males	CAS	219371	Ribeira Banzu*	44.2
		219372		45.6
		219373		38.4
		219374		34.7
		219377		41.8
		219378		42.8
		219379		44.5
		219380		43.35
		219381		42
		219382		41.2
		219400		35
	BMNH***	2000.59	"Pico de Principe" 600 m*.	43.8
		2000.60		41.4
juv.	CAS	219375		23
		219376		21.9
		219383		22
metamorphs		219370		11.0 – Gosner stage 45
		219397		10.5 – Gosner stage 46
		219398		11.6 – Gosner stage 46
Females		219399		105
		219401		69.2
		219177	Tchipique	108
		219351	Rio Papagaio	88.8
	BMNH***	2000.58	"Pico de Principe" 700 m**	63.99 (oviducal eggs)

* We are reasonably certain that these localities are equivalent in spite of differences in our GPS coordinates(see text): CAS = 01 35 20.7 N, 007 22 46.3 E; Baillie (1999) = 01 37 11N, 007 22 52 E.

** This specimen was collected on the forest floor by Baillie at about 700 m during his first descent from Pico do Príncipe. The precise locality is unknown but if the estimate of elevation is correct, this is the highest known specimen (Baillie personal communication).

*** Non–CAS Specimens examined: BMNH 2000.58. Female. Pico do Principe, Principe, 700 m. Sept 1, 1999. col. J.E.M. Bailie; BMNH 2000.59-60. Males. Pico do Principe, Principe 600 m. Sept. 1, 1999. col. J.E.M. Baillie.

TABLE 2. Size disparity between male and female *Leptopelis* in species where females are greater than 20 mm in snout-vent length than males; comparative snout-vent maxima taken from Schiøtz, 1999.

Species	*Maximum male SVL (mm)*	*Maximum female SVL (mm)*	*Maximum male SVL as % of max. female SVL*
Leptopelis palmatus	45.6	110	41
L. macrotis	46	84	45
L. millsoni	49	87	56
L. vermiculatus	50	85	58
L. boulengeri	48	81	59
L. occidentalis	43	71	60

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New Data on Tropical Eastern Pacific Chromodorididae (Nudibranchia: Doridina) with Description of a New Species of *Mexichromis* Bertsch, 1977

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Specimens of a small red-spotted species of chromodorid have been collected from southern México, Costa Rica, Panamá, Malpelo Island, Colombia and the Galápagos Islands. Comparison with described species reveals that they are juveniles of *Chromodoris baumanni* Bertsch, 1970. Specimens studied here exhibit considerable variation both ontogenetically and geographically. Mature specimens share characteristics with species attributed to the genus *Glossodoris*, and the systematic status of this species is reviewed and revised. Another species of chromodorid nudibranch is described from the tropical eastern Pacific. *Mexichromis tica* sp. nov. has been collected from Costa Rica and the Galápagos Islands. It differs from other eastern Pacific, Atlantic, and Indo-Pacific species in the genus in several important regards: (1) it has a white body color with a medial opaque white line and successive submarginal opaque white and orange marginal bands; (2) it has few large mantle glands distributed along the entire mantle margin; and (3) it has a vestigial rachidian row of teeth and variously denticulate inner, middle and outer lateral radular teeth.

Resumen

Ejemplares de una especie de cromodórido de pequeño tamaño con puntos rojos han sido recolectados en el sur de México, Costa Rica, Panamá, Isla Malpelo, Colombia e Islas Galápagos. Comparaciones detalladas con otras especies descritas muestran que son especimenes juveniles de *Chromodoris baumanni* Bertsch, 1970. Los ejemplares estudiados presentan una considerable variabilidad ontogenética y geográfica. Los ejemplares maduros comparten características atribuidas al género *Glossodoris* y el estatus taxonómico de ésta especie es revisado y discutido. Otra especie de nudibranquio cromodórido se describe del Pacífico Este tropical. *Mexichromis tica* sp. nov. ha sido recolectada en Costa Rica y las Islas Galápagos. Se diferencia de otras especies del género del Pacífico Este, Atlántico e Indopacífico por varios aspectos importantes: (1) Esta especie tiene un cuerpo blanco con una línea blanca opaca media y sucesivas bandas submarginales blanco opaco y naranja; (2) glándulas del manto de gran tamaño distribuidas por todo el borde del manto; (3) y una fila de dientes radulares raquídeos vestigiales así como varios dientes medios y marginales denticulados.

The chromodorid nudibranchs of the eastern Pacific Ocean have been reviewed by Bertsch (1977, 1978a–c). Since then only four additional species of chromodorid have been described from the eastern Pacific (Gosliner and Bertsch 1988; Ortea, Bacallado and Valdés 1992). Gosliner and Bertsch (1988) described *Mexichromis amalguae* from the Pacific coast of Baja California. Ortea et al. (1992) described three new species, *Berlanguella scopae*, *Chromodoris ruzafai* and *Thorunna talaverai* from the Galápagos. They also identified specimens of another chromodorid from the Galápagos Archipelago as supposedly *Noumea haliclona* (Burn, 1957). This species bears a striking resemblance to specimens of *Chromodoris baumanni* Bertsch, 1970, and its status is discussed here. Our recent field collections from Costa Rica, Baja California, the Galápagos Islands, and Panamá have provided additional material of this species. Detailed anatomical examination of variation in this species is warranted in order to evaluate its systematic status. A second species, collected from Costa Rica and the Galápagos, appears to be undescribed. Its external morphology differs markedly from other described eastern Pacific chromodorids. This paper describes and reviews the systematic placement of these two species.

Species Descriptions

***Mexichromis tica* Gosliner, Ortea, and Valdés, sp. nov.**
(Figs. 1A, 2–3)

Type material.— Holotype: CASIZ 170938, NE side Isla Darwin, Islas Galápagos, Ecuador, 23 m depth, 13 May 1994, leg. T.M. Gosliner. Paratypes: CASIZ 097511, one specimen, dissected, NE side Isla Darwin, Islas Galápagos, Ecuador, 23 m depth, 13 May 1994, leg. T.M. Gosliner. INBIO CRI 001486639, two specimens, dissected, Bajo del Diablo, Isla del Caño, Costa Rica, 18 April 1996, leg. E. Mollo.

Etymology.— *Mexichromis tica* is named for the vernacular name "tico," which signifies a native of Costa Rica.

Distribution.— This species is known from Costa Rica and the Galápagos Islands (present study).

External morphology.— The living animals (Fig. 1A) are translucent white. The pink viscera, showing through the translucent white dorsum, give the animal an overall pinkish appearance. A broad, opaque, white longitudinal band extends mid-dorsally from between the rhinophores to the anterior edge of the branchial cavity. The mantle margin is translucent white. A broad, opaque, white band is present submarginally along the mantle edge. Inside the white band, there is a band of orange or yellow that may be either continuous or interrupted. The posterior end of the foot is translucent white with a medial white stripe. An orange spot is present near the middle of the white stripe. The rhinophores have a translucent white base and an orange apex. The gill pinnae are uniformly translucent white.

Living animals are 3–6 mm in length. The dorsal surface of the mantle is covered with minute conical tubercles. The mantle is elongately oval and straight along its entire edge. The margin that overhangs the body is wide, nearly half of the total mantle width. The posterior end of the foot is triangular and extends some distance behind the posterior end of the mantle. Around the mantle margin are several rows of large, irregularly-shaped mantle glands (Fig. 3A). The glands of the largest specimen are more numerous with smaller glands situated between the larger ones. Triangular spicules are visible between the mantle glands around the margins of the mantle. The rhinophore stalk is short and the bulb bears 7–10 lamellae in the specimens examined. There are 4 unipinnate to bipinnate branchial leaves in the material examined. The foot is relatively narrow. The head and mouth are well-developed with a triangular oral tentacle on either side of the mouth.

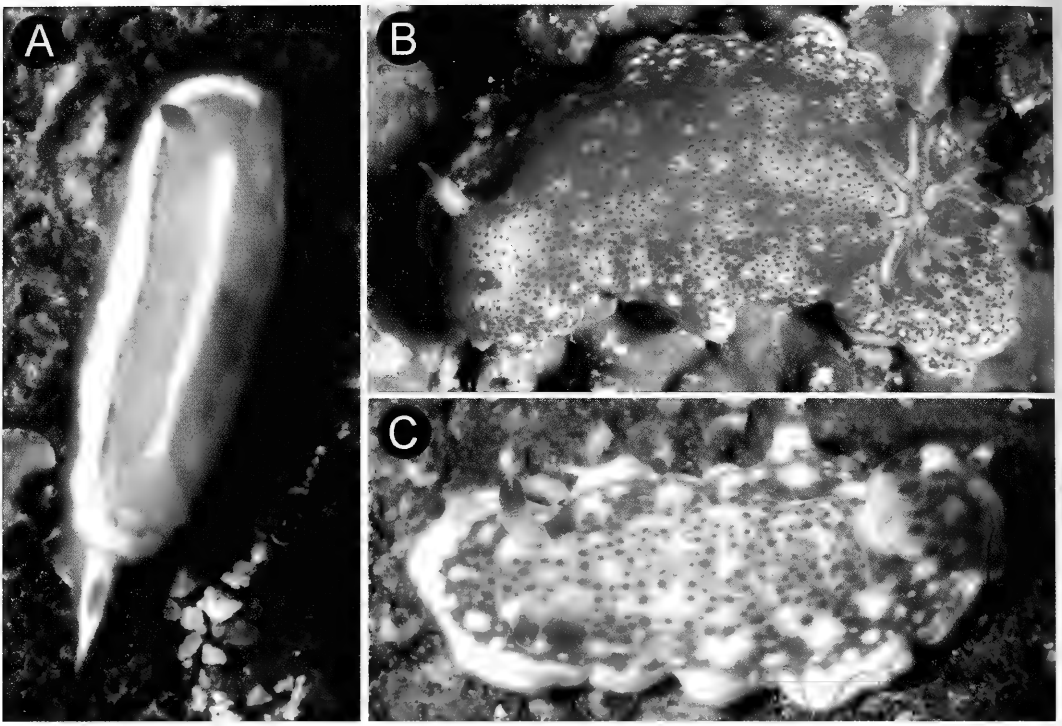

FIGURE 1. Living animals. A. *Mexichromis tica* sp. nov, holotype (CASIZ 097511), from Isla Wolf, Galápagos Islands, photo by T.M. Gosliner. B. *Glossodoris baumanni* (Bertsch, 1970), adult specimen, 33 mm length, from San Pedrillo, Costa Rica, photo by T.M. Gosliner. C. *Glossodoris baumanni* (Bertsch, 1970), juvenile specimen, 12 mm length, from San Pedrillo, Costa Rica, photo by T.M. Gosliner.

BUCCAL ARMATURE.— At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 2D) are short and broad with a broad apex bearing 3–7 irregular shaped denticles. The radular formula is difficult to determine owing to the broadly overlapping teeth. A vestigial rachidian row of teeth is present in one specimen (CASIZ 097511, Fig. 2A), but it appears to be absent in the other two individuals examined (INBIO CRI 001486639). The rachidian row of teeth in the one specimen consists of teeth with only a short narrow cusp. The innermost lateral teeth (Fig. 2A) have a broad base with a series of 4–6 curved, triangular denticles along the inner margin. There is no primary cusp and most of the denticles are equal in size with the exception of the outermost, which is smaller than the others. The lateral teeth from the middle of the radular row are short and curved (Fig. 2C) and bear 4–6 curved, triangular denticles on the outer side of the teeth. The more basal denticles are smaller than the others, but there is no primary cusp on any of these teeth (acuspidate, *sensu* Bertsch, 1977). The 4–5 outermost lateral teeth (Fig. 2B) are broad and spatulate and are thinly chitinized. They bear 16–20 thin, elongate denticles along the margin.

REPRODUCTIVE SYSTEM.— (Fig. 3B) The ampulla is short, thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens curves over the bursa copulatrix and narrows into a short ejaculatory segment. This muscular portion narrows and again widens into the short penial bulb. The penial bulb shares a common atrium with the vagina. The distal end of the vas deferens is devoid of penial hooks. The female gland mass consists of the

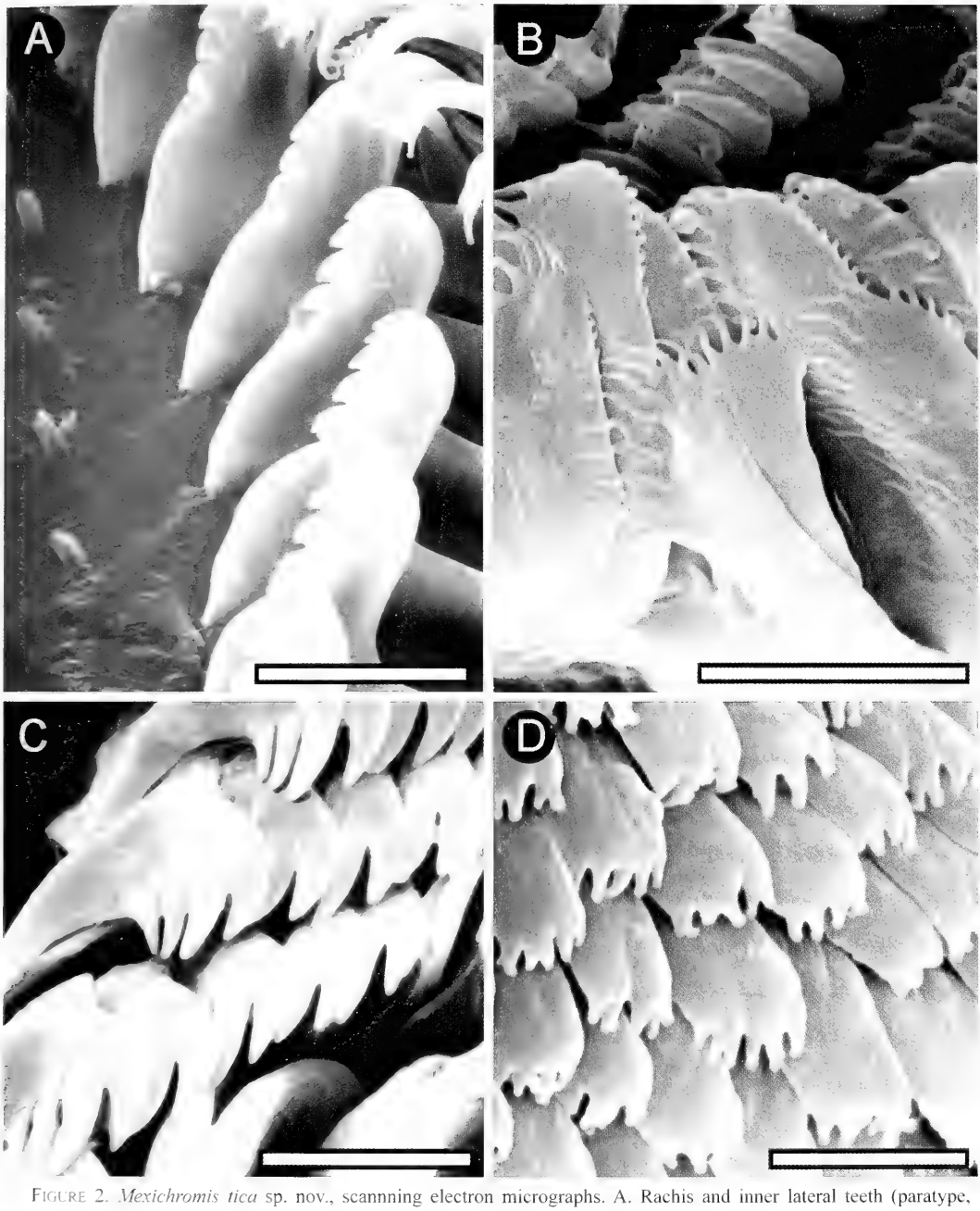

FIGURE 2. *Mexichromis tica* sp. nov., scannning electron micrographs. A. Rachis and inner lateral teeth (paratype, CASIZ 097511), scale bar = 10 μm. B. Outer lateral teeth, (paratype, CASIZ 097511), scale bar = 10 μm. C. Lateral teeth from the central portion of half-row, (paratype, CASIZ 097511), scale bar = 7.5 μm. D. Jaw rodlets, (paratype, INBIO CRI 001486639), scale bar = 5 μm.

large mucous gland and smaller membrane and albumen glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. The vagina is relatively thin and straight. It is widest nearest its junction with the penis. The elongate, club-shaped receptaculum seminis has a recurved duct that

joins directly to the base of the thin-walled, spherical bursa copulatrix. The vagina emerges near the base of the bursa. The thin uterine duct emerges from the middle of the thin vagina. The uterine duct is short and curved and enters the female gland mass near the albumen gland.

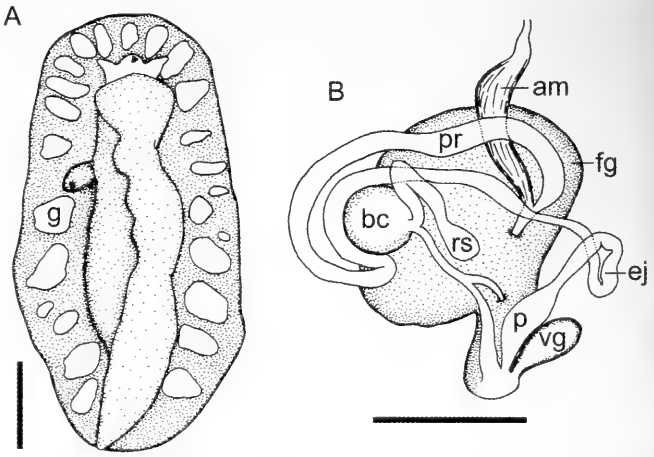

FIGURE 3. *Mexichromis tica* sp. nov., A. Ventral view of holotype (CASIZ 097511) showing distribution of mantle glands, g = mantle gland, scale bar = 2 mm. B. Reproductive system, am = ampulla; bc = bursa copulatrix; ej = ejaculatory duct; fg = female gland mass; p = penis; pr = prostate; rs = receptaculum seminis; vg = vestibular gland, scale bar = 1 mm.

DISCUSSION.— Rudman (1984) reviewed the genera of chromodorid nudibranchs and concluded that *Mexichromis* Bertsch, 1977, represents a valid genus. *Mexichromis* is characterized by having a few large mantle glands, acuspidate (Bertsch 1977) or multicuspidate (Rudman 1984) radular teeth, and a ramified vestibular gland (Rudman 1984). In the eastern Pacific, *Mexichromis* is represented by *M. antonii* (Bertsch, 1976), *M. porterae* (Cockerell, 1901), *M. tura* (Marcus and Marcus, 1967) and *M. amalguae* Gosliner and Bertsch, 1988.

Mexichromis francoisae (Bouchet, in Bouchet and Ortea, 1980) is known from the eastern Atlantic of Senegal (Bouchet and Ortea 1980) and the Cape Verde Islands (Ortea 1988). This species was transferred to the genus *Mexichromis* by Ortea et al. (1996). Ortea et al. (1996)also described *M. molloi* Ortea and Valdés, 1996, from Venezuela. These eastern Pacific and Atlantic species all have a blue ground color with yellow or white longitudinal lines or marginal bands. Rudman (1984) suggested that *Chromodoris kempfi* Marcus, 1970, may be a species of *Mexichromis*, but little is known of its anatomy. Its greenish body color with a yellow marginal band with black markings differs markedly from the color of *M. tica*.

Several Indo-Pacific species, *M. festiva* (Angas, 1864), *M. mariei* (Crosse, 1872), *M. macropus* Rudman, 1983, and *M. multituberculata* (Baba, 1953), have an opaque white body color with large purple tubercles on the notum. Additional purple, yellow or orange pigment may also be present.

The color pattern of *M. tica*, with a transluscent white ground color with opaque white and yellow submarginal bands, is unique for this species. Of the species of *Mexichromis* that have been studied, only *M. amalguae* and *M. tica* are known to possess a vestigial rachidian tooth. However, a rachdian row of teeth may be present or absent in *M. tica*. *Mexichromis tica* is unique among members of *Mexichromis* in having multidenticulate to pectinate outer lateral teeth. In the remaining taxa, the outer lateral teeth are similar in shape to the midlateral teeth.

The reproductive system has been described in detail for *Mexchromis macropus*, *M. porterae*, *M. tura*, *M. francoisae*, *M. molloi*, and *M. amalguae* (Rudman 1984; Gosliner and Bertsch 1988; Ortea et al. 1996). In these six species, the vestibular gland consists of multiple lobes, whereas in *M. tica* it is simply ovoid.

Inclusion of *M. tica* in *Mexichromis* requires modifying the boundaries of the taxon to include species with pectinate outer lateral teeth and a simple vestibular gland. *Mexichromis tica* is tenta-

tively placed in *Mexichromis* until a more comprehensive phylogenetic study of the Chromodoridiae is undertaken.

***Glossodoris baumanni* (Bertsch, 1970)**
(Figs. 1B–C, 4–5)

Chromodoris norrisi Farmer, 1963: Marcus and Marcus, 1967:170–173, fig. 24, misidentification.
Chromodoris baumanni Bertsch, 1970:8, figs. 3–13; Sphon and Mulliner, 1972:150; Bertsch, 1978a:307, fig. 3a, 4, 10–12; Bertsch, in Kerstitch, 1991:57; Debelius, 1996:212, lower figure.
Noumea haliclona (Burn, 1957): Ortea, Bacallado and Valdés, 1992:62–65, figs. 19–20, pl. 1E, misidentification.
Glossodoris baumanni, (Bertsch, 1970), comb. nov.

Material examined.— CASIZ 074004, one specimen, dissected, s side of Pulmo Point, Cabo Pulmo, Baja California Sur, México, 13 m. depth, 22 January 1984, leg. H. Bertsch and L. Aguilar. INBIO CRI 001486926, one specimen, Bahía Hachal, Costa Rica, 8 December 1995. INBIO CRI 001486927, two specimens, Punta Uvita, Costa Rica, 14 April 1996. CASIZ 075179, one specimen, Isla del Coco, Costa Rica, 13 m. depth, 24 March 1989, leg. K. Kaiser WAM 102-95, one specimen, Isla de Cocos, Costa Rica, 28 March 1997, leg. C. Bryce. WAM 106-95, one specimen, Isla de Cocos, Costa Rica, 23 March 1997, leg. K. Kaiser. CASIZ 088147, five specimens, one dissected, sea stack, off Isla Ladrones, Gulf of Chriquí, Panamá, 14 m. depth, 14 April 1993, leg. T.M. Gosliner. CASIZ 088150, three specimens, Punta David, se side of Isla Jicarón, Gulf of Chiriquí, Panamá, 13 m. depth, 17 April 1993, T.M. Gosliner. CASIZ 088203, four specimens, point W of anchorage, Islas Secas, Gulf of Chiriquí, Panamá, 13 m. depth, 22 April 1993, leg. T.M. Gosliner. CASIZ 088227, one specimen, off Rocas Tiburón, off Isla Brincano, Gulf of Chiriquí, Panamá, 23 April 1993, leg. T.M. Gosliner. CASIZ 088161, two specimens, se side of Isla Jicarón, Gulf of Chiriquí, Panamá, 16 April 1993, leg. T.M. Gosliner. CASIZ 097512, one specimen, NE side Isla Darwin, Islas Galápagos, Ecuador, 22 m. depth, 13 May 1994, leg. T.M. Gosliner. CASIZ 071429, one specimen, Isla Santiago, Islas Galápagos, Ecuador, intertidal zone, 19 February 1988, leg. K. Kaiser. WAM S1164, one specimen, Isla Malpelo, Colombia, 13 m depth, 26 March 1998, leg. C. Bryce. One specimen, Puerto Egas, Isla Santiago, Islas Galápagos, 18 March 1991, leg. J. Ortea. One specimen , Isla Genovesa, Islas Galápagos, 8 March 1991, leg. J. Ortea.

Distribution.— This species is known from the Gulf of California, Baja California Sur (Bertsch, 1970, 1978a; present study) México; Sayulita, Nayarit, México; several localities in Costa Rica, Panamá, the Galápagos Islands and from Isla Malpelo, Colombia (present study).

Natural history.— *Glossodoris baumanni* is found in relatively shallow water on rocky reefs. In Costa Rica and Panamá, it is one of the most commonly occurring opisthobranchs from the intertidal zone to 20 meters depth.

External morphology.— The living animals (Fig. 1B–C) are brightly colored with a network of purple to red and opaque white pigment. There is a broad yellowish white or light gray band around the mantle, just inside the translucent white margin. The inside edge of the white border is very irregular and slightly convoluted with opaque white, with 1–5 rows of rounded mantle glands extending into the brick red central part of the body (Fig. 1C). There are numerous purplish red spots, each surrounded by a broad purple-gray or yellowish ring all over the central brick red patchwork. Specimens from Baja California generally lack red pigment between the red spots and the notum is opaque white. More mature specimens south of Baja California have dense red pigment between the red spots (Fig. 1B). An identical pattern is present on the surface of the foot. The

majority of these spots are joined together forming patches of varying sizes. The rhinophores have an opaque white base and a broad purple band just below the opaque white apex. The gill pinnae are also opaque white with purple apices. Scattered red pigment spots are present on the innner and outer surfaces of the gill rachis.

The living animals are 9–65 mm in length. The mantle is elongately ovoid and folds down over the sides of the body forming a series of permanent undulations of the mantle edge. These undulations are more pronounced in more mature specimens. The margin that overhangs the body is wide, nearly half of the total mantle width. The posterior end of the foot is triangular and extends some distance behind the posterior end of the mantle. Immediately interior to the mantle margin are 1–5 rows of irregularly distributed, rounded mantle glands (Fig. 5A). The mantle glands are more dense and smaller near the margin. The interior glands are larger and have an irregular lobed shape. The rhinophore stalk has 9–22 lamellae in the specimens examined. There are 6–15 unipinnate branchial leaves in the material examined. In some of the larger speciments a few of the posterior gills are not entirely separate to the base, but have been counted as distinct gill branches. In the larger specimens the branchial leaves form a spiral on either side and the gill has been observed to vibrate slowly.

Buccal armature.— The muscular portion of the buccal mass is approximately equal in length to the oral tube. At the anterior end of the muscular portion of the buccal mass is the chitinous labial cuticle, which bears numerous jaw rodlets. The rodlets (Fig. 4D) are elongate, curved and have a bifid apex. The radular formula is 61 × 39.1.39. in one 20 mm specimen examined (CASIZ 088203) and a 12 mm specimen 33 × 21.0.20. A rachidian row of teeth is present in one specimen, but absent in the other four individuals examined. Examination of the holotype and paratype radula revealed similar variation in the presence and absence of a rachidian row of teeth, with the holotype lacking a rachdian row, while the paratype has a row of rachidian teeth. The innermost lateral teeth (Fig. 4A) are arched with a short cusp. There are 1–2 triangular denticles on the inner side of the tooth. The outer side has 1–3 denticles. In the radulae with the rachidian tooth present, it is apparent that the rachidian tooth actually represents a portion of the inner lateral tooth where the inner denticle was present. The second through fourth laterals have 3–4 denticles on the outer side of each tooth. The lateral teeth from the middle of the radular row are far more elongate (Fig. 4B) and bear 4–8 small, triangular denticles on the outer side of the teeth. The outermost lateral teeth (Fig. 4C) are elongate with 4–5 denticles situated near the top of the tooth.

Reproductive system.— (Fig. 5B) The ampulla is elongate, thick and tubular, narrowing somewhat before bifurcating into an oviduct and vas deferens. The short oviduct enters the female gland mass near the albumen gland. The proximal prostatic portion of the vas deferens is highly convoluted and extensive. It narrows somewhat as it develops into the muscular, ejaculatory portion. The ejaculatory portion is initially narrow and gradually widens and curves over the bursa copulatrix. It then contines with another series of loops and widens into the penial bulb. The penial bulb shares a common atrium with the vagina. The distal end of the vas deferens is devoid of any penial hooks. The female gland mass consists of the large mucous gland and smaller membrane and albumen glands. Near the exit of the mucous gland is a small, ovoid vestibular gland. The vagina is relatively thin, elongate and somewhat convoluted. It is muscular in the distal half and becomes glandular in the half closest to the genital aperture. The elongate, club-shaped receptaculum seminis joins directly to the base of thin-walled, spherical bursa copulatrix. The uterine duct and vagina both emerge near the base of the bursa. The uterine duct is short and curved and enters the female gland mass near the albumen gland.

Discussion.— Bertsch (1970) described *Chromodoris baumanni* from two specimens collected from Isla San Francisco and Isla Cerralvo, Baja Californiá, México. Subsequent authors have

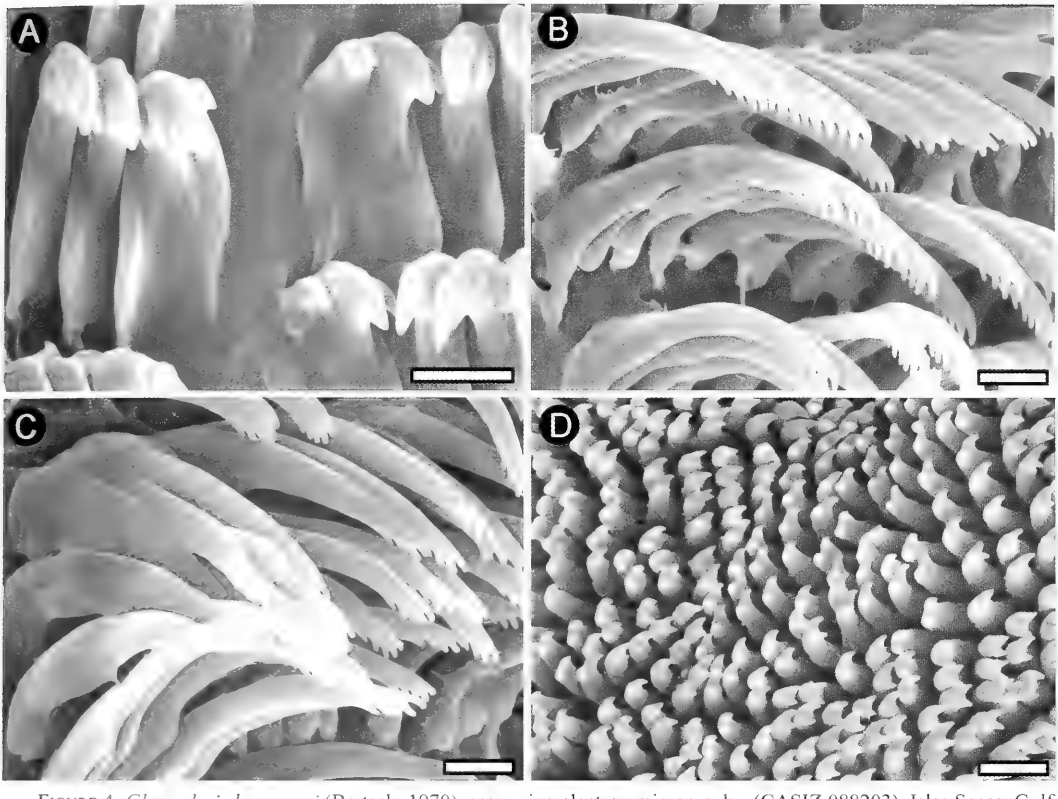

FIGURE 4. *Glossodoris baumanni* (Bertsch, 1970), scannning electron micrographs, (CASIZ 088203), Islas Secas, Gulf of Chiriquí, Panamá. A. Rachis and inner lateral teeth, scale bar = 10 μm. B. Midlateral teeth from the central portion of half-row, scale bar = 10 μm. C. Outer lateral teeth, scale bar = 10 μm. D. Jaw rodlets, scale bar = 10 μm.

identified additional material from other eastern Pacific localities from mainland México and the Galápagos Islands (Sphon and Mulliner 1972; Bertsch 1978a; Debelius 1996). More recently, Ortea et al. (1992) attributed specimens of this species from the Galápagos to *Noumea haliclona* (Burn, 1957). *Noumea haliclona* is a variably colored species that may be either pink or yellow in its body coloration and a few darker pink spots (Rudman 1983). Its rhinophores and gill are the same color as the body. This species is endemic to temperate southeastern Australia. In contrast,

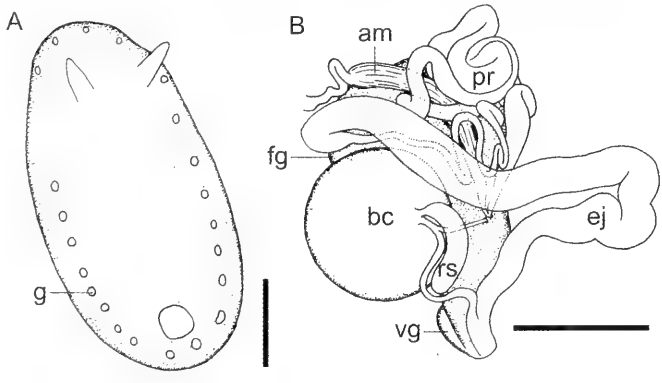

FIGURE 5. *Glossodoris baumanni* (Bertsch, 1970) A. Dorsal view of juvenile specimen showing distribution of mantle glands, g = mantle gland, scale bar = 2 mm.. B. Reproductive system of mature specimen, am = ampulla; bc = bursa copulatrix; ej = ejaculatory duct; fg = female gland mass; p = penis; pr = prostate; rs = receptaculum seminis; vg = vestibular gland, scale bar = 3 mm.

Chromodoris baumanni has more numerous, smaller red pigment spots and the rhinophores and gill branches are tipped with purple pigment. Internally, *N. haliclona* has a much broader innermost lateral teeth than *C. baumanni*, with much shorter jaw rodlets. *Noumea haliclona* has a digitate vestibular gland (Rudman 1984), while that of *C. baumanni* is simple. The anatomy of specimens of *C. baumanni* examined here is entirely consistent with material described by Ortea et al. (1992) from the Galápagos Islands, with one notable exception. The reproductive system of their specimen has a small female gland mass, indicating that their specimen was not sexually mature. There is little question that the specimens that Ortea et al. (1992) attributed to *N. haliclona* are in fact *C. baumanni*.

Rudman (1984) noted that *Glossodoris* was characterized by having a convoluted mantle margin, spirally arranged gill branches on either side of the gill, a gill that vibrates rhythmically, a radular ribbon with numerous rows that is much longer than wide and an elongate, thin vaginal duct. He also suggested that species of *Chromodoris* have a straight or temporarily convoluted mantle margin, a gill without spirally arranged branches, a more squarely-shaped radular ribbon and a short muscular vagina. The only species of *Chromodoris* that is known to vibrate its gill is *C. vibrata* (Pease, 1860) (Bertsch and Johnson 1981).

Specimens of *Chromodoris baumanni* have several characteristics that are similar to species attributed to *Glossodoris*. For instance, specimens of this species have a permanently, slightly convoluted mantle margin. Also, juvenile specimens of *C. baumanni* have fewer gill branches that do not form a spiral (Fig. 1C), whereas mature specimens have well-developed spirals (Fig. 1B). Larger specimens of *C. baumanni* have been observed to have a gill plume whose branches vibrate slowly (present study), although the gill moves more slowly than in members of *Glossodoris*. The shape of the radular ribbon of *C. baumanni* is not elongate with relatively few (32–84) rows of radular teeth (Bertsch 1978a; present study), as in most species of *Chromodoris*. Rudman (1986) described several species of *Glossodoris* that had a shorter radular ribbon with fewer rows of teeth than had previously been observed. Bertsch and Gosliner (1989) also documented the presence of relatively few radular rows in *Glossodoris poliahu* Bertsch and Gosliner, 1989 and *G. tomsmithi* Bertsch and Gosliner, 1989. The vaginal duct of *C. baumanni* is thin and elongate as in species of *Glossodoris* (Rudman, 1984).

Based on the fact that most of the anatomical details of *C. baumanni* are consistent with those described for species of *Glossodoris*, this species is placed in *Glossodoris*. Detailed phylogenetic studies are needed to determine monophyletic groups within the Chromodorididae. *Hypselodoris* is the only chromodorid taxon whose monophyly has been tested with a study of its species-level phylogeny (Gosliner and Johnson 1999). The hypotheses of relationships within the Chromodorididae proposed by Rudman (1984) and Gosliner and Johnson (1999) require additional detailed study and phylogenetic analysis to further define monophyletic groups within the highly diverse chromodorid nudibranchs.

Acknowledgments

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A New Species of *Oscarella* (Demospongiae: Plakinidae) from California

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We describe a new species of *Oscarella* Vosmaer, 1877 (Porifera: Homosclerophorida) from a rocky coast and marine aquariums in central California and analyze its spatial distribution and temporal fluctuations to determine if it is a non-indigenous species. We also compare the efficiency of two different fixatives, Bouin's solution and glutaraldehyde in seawater, and found that glutaraldehyde is better for comparisons of anatomical and cytological characters that are important for species identification.

This is the first record of the genus *Oscarella* from the Eastern Pacific. The new species is characterized by its light brown to rusty orange color, undulated appearance, bumpy, microlobate surface, soft, slimy consistency, two particular kinds of cells with inclusions, and occurrence in the intertidal high zone. It sometimes thrives in laboratory conditions, indicating that predators may limit its vertical distribution on the shore. The new species of *Oscarella* is clearly different in external morphology and cell content from all previously described species of *Oscarella*, thus giving low support to the hypothesis that it is an invasive species. Instead, it appears to have been previously overlooked because it is inconspicuous and relatively uncommon in the field, and because it could not be distinguished from *Halisarca sacra* de Laubenfels, 1930 or *Halisarca* sp. in keys to the West Coast sponge fauna. We present how it can be distinguished from *Halisarca*, and discuss the present knowledge of that genus in the northeast Pacific in comparison to *Oscarella*.

KEY WORDS: California, *Halisarca*, Homosclerophorida, intertidal, *Oscarella*, Porifera, sponge.

Marine invasive species often appear first in aquariums, to be later established in the field. A classic marine example is the alga *Caulerpa taxifolia* in the Mediterranean, but there are many others (e.g., Ribera and Boudouresque 1995). In the mid 1980s, an unidentified slimy sponge without skeleton (either spongin or spicules) appeared growing on submerged rocks and the sides of aquariums and sea tables at the Joseph M. Long Marine Laboratory of the University of California, Santa Cruz, on the northern edge of Monterey Bay. At first, it was taken to be a species of *Halisarca* Johnston, 1842, the only similar organism in the main key for intertidal sponges of central California (Hartman 1975). However, in 1990, M. Cristina Diaz examined a piece of the sponge with scanning electron microscopy and identified it as a member of the genus *Oscarella* Vosmaer, 1887 (Demospongiae: Plakinidae) (Diaz and van Soest 1994), a genus mainly known in the Mediterranean and previously unknown from the eastern Pacific. The sponge was noticed in the

late 1980s in several of the exhibit tanks of the Monterey Bay Aquarium, which is located on the southern side of Monterey Bay, and at Long Marine Laboratory, where it continues to be present (JSP, pers. obs.). It also became established in the exhibit tanks and teaching labs of the Seymour Marine Discovery Center, adjacent to Long Marine Laboratory, shortly after it opened in 2000. After seeing the sponge at these facilitates in early 2004, Scott Nichols (pers. commun.) found the same sponge in an aquarium at the Bodega Marine Laboratory of the University of California, Davis.

In addition to the question of its identity, it was puzzling that the sponge had not been seen in the field, especially since field biologists have been working in the rocky intertidal of the Monterey Bay area of central California throughout the 20th century. Moreover, de Laubenfels (1932) had extensively monographed the sponges of California. Finally, in September 2002, one of us (JSP) found the sponge growing on the sides and undersurfaces of intertidal rocks on the northwest corner of Carmel Point, in Carmel Bay, central California (Figs. 1, 2A).

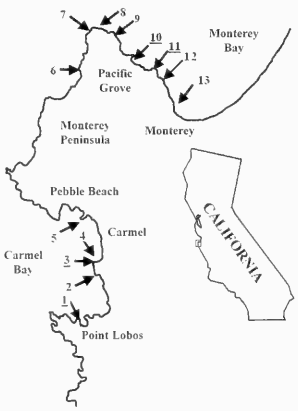

FIGURE 1. Map of Carmel Bay and the Monterey Peninsula showing the location of 13 intertidal sites examined between September 2002 and May 2004; underlined numbers indicate sites where specimens of *O. carmela* sp. nov. were found. 1. Whaler's Cove, Point Lobos State Park; 2. Carmel Point, southwest corner; 3. Carmel Point, northwest corner; 4. Carmel Point, north side, between site 3 and Carmel Beach; 5. Arrowhead Point on east side of Stillwater Cove; 6. Asilomar State Beach State Park, south end next to Spanish Bay Beach; 7. The Great Tide Pool, south of Point Pinos; 8. Point Pinos; 9. Lucas Point, between Coral Street and Esplande Park; 10. Lovers Point, east side, both sides of Lovers Point Beach; 11. Hopkins Marine Station (Cabrillo Point); 12. Monterey Bay Aquarium (Point Alones), underneath building; 13. Monterey Harbor, between the Coast Guard Pier and Fisherman's Wharf. Square on inserted map of California outlines the Monterey Peninsula and Carmel Bay.

Most species of *Oscarella* have been described from the Mediterranean, but there are also two Indo-Pacific species and a few doubtful Australian and South African records (e.g., Boury-Esnault et al. 1992; Muricy et al. 1996; Muricy and Diaz 2002; Bergquist and Kelly 2004). Moreover, many species of *Oscarella* occur in Brazil and the Caribbean (GM, pers. obs.), but to a large extent they are uncommon and most have yet to be described. The same might be true for California, and this is likely an undescribed species indigenous to this area. However, with no previous records of the genus *Oscarella* along the Pacific coast of North America, the question arises whether it could have been introduced from elsewhere, possibly via disposal of aquarium water. If it is non-indigenous, it is not a very attractive addition to the Californian fauna: it is a tan, bumpy, slime-like sponge that overgrows other organisms. If it is conspecific with any of the Mediterranean species of *Oscarella*, that would support the invasion hypothesis, and there is a risk that it could disrupt natural biotas.

Our goals were to determine whether this skeleton-less sponge belongs to *Oscarella* or *Halisarca*, and whether it is a new species, either indigenous but unnoticed before or introduced but undescribed, or a known species introduced from somewhere else. We also analyzed the spatio-temporal distribution of the species in the Monterey Bay region, and compared the efficiency of two different fixatives, Bouin's solution and glutaraldehyde in seawater, for the histology and taxonomy of these skeleton-less sponges.

MATERIALS AND METHODS

Specimens were photographed with an Olympus Camedia 3040 digital camera and collected in November 2002 and May 2003 from rocks in a high intertidal pool at Carmel Point in Carmel

Bay, central California (Figs. 1, 2A). Additional specimens were collected from tanks in Long Marine Laboratory and the Seymour Marine Discovery Center of the University of California, Santa Cruz (UCSC). Small pieces of the sponges were collected with a pocketknife and immediately fixed in Bouin's fixative (75 ml saturated aqueous solution of picric acid: 25 ml 37–40% formalin (formaldehyde): 5 ml glacial acetic acid) or freshly prepared 2.5% glutaraldehyde in seawater (25% glutaraldehyde diluted and buffered with seawater). Bouin's-fixed samples were embedded in paraffin for thick sections and epon resin for semithin sections. Glutaraldehyde-fixed samples were post-fixed in 1% osmium tetroxide and embedded in epon resin for semithin and ultrathin sections. Thick and semithin sections were stained with toluidin blue or acid fucsin, observed in light microscopy (LM), and photographed with a Nikon Coolpix 4500 digital camera. Ultrathin sections were stained with uranyl acetate, contrasted with lead citrate and observed in a Zeiss M900 transmission electron microscope (TEM).

Systematics

Phylum Porifera Grant, 1836
Class Demospongiae Sollas, 1885
Subclass Homoscleromorpha Lévi, 1973
Order Homosclerophorida Dendy, 1905
Family Plakinidae Schulze, 1880

Genus *Oscarella* Vosmaer, 1887

Type species: *Halisarca lobularis* Schmidt, 1862 (by monotypy).

[*Oscaria*] Vosmaer, 1881: 163 (preocc. by Oscaria Gray, 1873 – Reptilia);
Oscarella Vosmaer, 1884: pl. 8 (explanation); 1887: 326 (nom. nov. for *Oscaria* Vosmaer).
Octavella Tuzet and Paris, 1964: 88.

Diagnosis (Muricy and Diaz 2002).— Plakinidae without skeleton, with thinly encrusting to lobate shape. Thin ectosome (< 100 μm), often limited to pinacoderm; true cortex absent. Mesohyl poorly developed, with a proportion of mesohyl to chambers varying from 0.5:1 to 1.2:1. The aquiferous system has a sylleibid organization, with spherical, eurypylous choanocyte chambers uniformly arranged around large, regular exhalant canals, and a large basal cavity.

Oscarella carmela Muricy and Pearse, sp. nov.

(Figs. 2–4)

Diagnosis.— Intertidal or aquarium-dwelling *Oscarella,* light brown to tan or rusty orange in color, with bumpy, microlobate surface, wavy appearance, soft, slimy consistency, and two particular kinds of cells with inclusions (types 1 and 2).

Material examined.— (12, all from central California, USA) (MNRJ, Museu Nacional, Universidade Federal do Rio de Janeiro; CASIZ, California Academy of Sciences; SBMNH, Santa Barbara Museum of Natural History)

Holotype: MNRJ 8033, Carmel Point, Carmel Bay, intertidal, J. Pearse coll., 08 May 2003. Paratypes: MNRJ 8032, 07 November 2002, CASIZ 168925, 08 May 2003, Carmel Point, Carmel Bay, central California, intertidal, J. Pearse coll.; MNRJ 8034, 8035, CASIZ 168924, 06 November 2002, SBMNH 354351 (three specimens) 29 July 2004, tanks in Long Marine Laboratory, UCSC, Santa Cruz, J. Pearse coll.; MNRJ 8031 (three specimens), 06 November 2002, teaching lab of the Seymour Marine Discovery Center, UCSC, Santa Cruz, J. Pearse coll.

Description.— Thinly encrusting, irregular sponges, generally light brown, up to 20–30 cm

in diameter, with extremely soft, slimy consistency. Thickness, color, and surface irregularities variable. Most specimens tan in color, 2–3 mm thick, and lumpy or undulated with conspicuous channels and oscula (Fig. 2B–F). Some specimens gray-tan and smoother, or pale brown to rusty orange, with very bumpy surfaces and orange blotches. These different morphologies could be ecophenotypes or different stages of growth. In some cases, one morphology graded into another in what appeared to be the same individual. On the glass walls of aquariums, the sponge is nearly transparent and clusters of choanocyte chambers and spherical embryos can be seen inside. The sponge is easy to peel off smooth surfaces. Under low magnification (60×) the colored spherical choanocyte chambers can be seen in living material, and often, the colorless spherical hollow embryos.

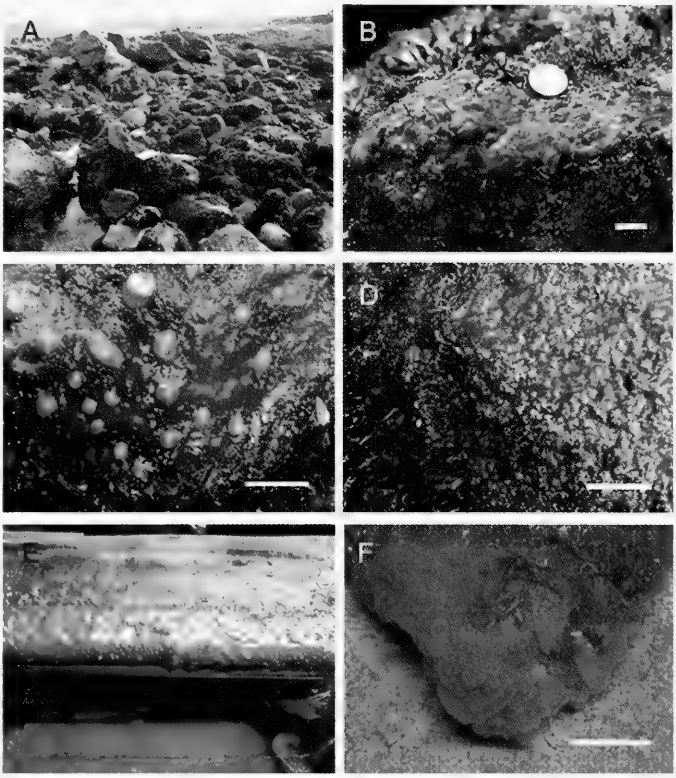

FIGURE 2. *Oscarella carmela* sp. nov. A. Habitat at the northwest corner of Carmel Point, with boulders in the intertidal zone. B-D. Three colonies on the upturned sides of boulders exposed during low tide; colonies of the bryozoan *Eurystomela bilabiata* partially overgrown in B, polyps of the corallimorpharian *Corynactis californica* partially surrounded in C (scale bar = 2 cm; coin in B is a U.S. quarter). E. Colony growing up to the water line on the side of a 8 cm high plastic box in an aquarium in Long Marine Lab. F. Colony growing on a rock in an aquarium in the Seymour Marine Discovery Center; the sponge is covered with seawater (scale bar = 2 cm).

ANATOMY.— Because glutaraldehyde provided better fixation for fine structure than Bouin's solution (see below), the description of anatomy and cytology is based on glutaraldehyde-fixed material. Choanocyte chambers ovoid to spherical eurypilous, 25–65 μm in diameter, organized around large exhalant canals (Fig. 3A–G). Mesohyl between the chambers very thin (5–10 μm thick). Proportion of mesohyl to chamber volume less than 0.5:1.0. Ectosome thin, 5–10 μm thick. Basal cavities large, separated by septa without choanocyte chambers, 10 μm thick. Cinctoblastula larvae characteristic of the family Plakinidae, 50–300 μm in diameter (Fig. 3H).

CYTOLOGY.— Choanocytes ovoid to pyramidal, irregular, 2–5 μm in diameter by 3–5 μm high (Fig. 4A–C). Nucleus basal or apical, 1.5–2.2 μm in diameter. Cytoplasm with up to eight phagosomes, 0.5–1.5 μm wide. Choanocyte collars with 25–33 microvilli. Apopylar cells not observed. Pinacocytes flat or elongated to ovoid, 5–10 μm long by 0.5–2 μm wide, flagellated, anchored in the mesohyl by short pseudopodia (Fig. 4C–D). Nucleus ovoid, 1–2 μm in diameter, nucleolated. Cyto-plasm with numerous small phagosomes, 0.3–0.7 μm, and often also one larger vacuole with clear contents. Choanoderm and pinacoderm lined by a basement membrane-like structure, which is a continuous, 5–10 nm thick layer of condensed collagen fibrils in the mesohyl closely adjacent

to the base of the cells. Collagen deposition in the mesohyl heterogeneous (Fig. 4D). As seen in both LM and TEM, ameboid cells of the mesohyl include archaeocytes and two types of cells with inclusions. Archaeocytes roughly ovoid, irregular, 5.0 × 3.5 μm, with abundant pseudopodia (Fig. 4E, F). Cytoplasm filled with phagosomes 0.3–1.5 μm wide containing food particles, including bacteria, in various stages of digestion. Nucleus ovoid or irregular, 1.0–2.5 μm, nucleolated. Type 1 cells with inclusions ovoid, 5.0 × 3.0 μm, irregular, with short pseudopodia (Fig. 4E). Nucleus 2 μm in diameter, ovoid or compressed by the abundant cytoplasmic inclusions. Cytoplasm filled with inclusions of two kinds, 0.2–1.0 μm wide, one kind with relatively dark and homogeneous contents and the other with clear, heterogeneous, filamentous contents. Type 2 cells with inclusions have irregular shape, 5.0×3.0 μm, rarely with short pseudopodia (Fig. 4F, G). Cytoplasm with 5–15, 0.5–2.0 μm wide inclusions with homogeneous contents, and 3–8 larger vacuoles, 1–4 μm in diameter, with clear and filamentous contents. Nucleus 1.2–2.5 μm in diameter, ovoid or compressed by abundant cytoplasmic inclusions. This cell type appears to be involved in the secretion of ground substances of the intercellular matrix, because it is often seen liberating the contents of its larger, clear vacuoles in the mesohyl (Fig. 4G). Endobiont bacteria of two kinds (Fig. 4H): type B1 most common, ovoid, 1.0–1.5 by 0.6–1.0 μm, with a wrinkled cell wall, a clear and filamentous nuclear region and a darker cytoplasmic region; type B2 rod-like, 1.0 × 0.2 μm, with darker and rather homogeneous contents, and without a clear distinction between nuclear and cytoplasmic regions.

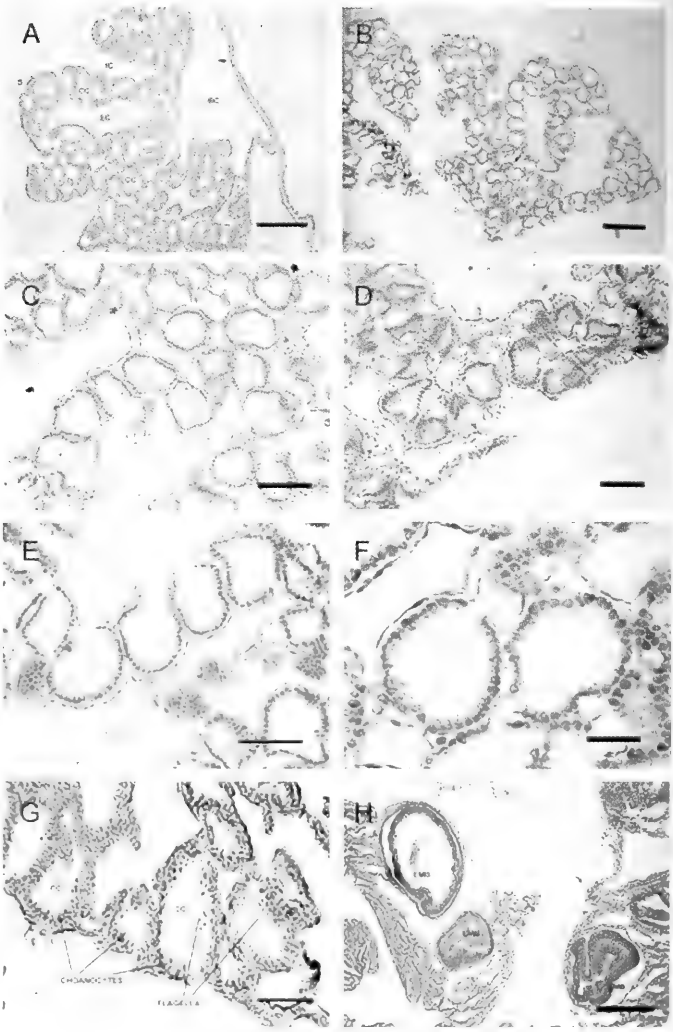

FIGURE 3. Histology of *Oscarella carmela* sp. nov. (LM). (A–B) transverse section showing the arrangement of choanocyte chambers around exhalant canals and the large basal cavities (scale bar = 100 μm); (C–E) choanosome (scale bars = 50 μm); (F–G) choanocyte chambers (scale bars = 25 μm); (H) embryos (scale bar = 100 μm). Fixation: A, G and H, Bouin's fixative; B–F, glutaraldehyde / osmium tetroxide.

ECOLOGY.— Specimens of *Oscarella carmela* occur as thin sheets on the sides of granite outcrops and on the edges and undersurface of boulders in high-zone tide pools of Carmel Bay and the

Monterey Peninsula (Fig. 1, Fig 2A). These sponges apparently need to remain continually immersed, but do well in the variable environment of high-tide pools. The tops of the boulders in this habitat supported typical high-zone algae (*Silvetia compressa, Fucus gardneri, Endocladia muricata, Mazzaella affinis, Mastocarpus* spp.) whereas the sides of boulders immersed in the tide pools often were covered with the red alga, *Prionitis lanceolata,* and encrusting and upright coralline algae. The undersurfaces of the boulders supported a rich variety of sessile and encrusting animals, e.g., red poecilosclerid sponges, cnidarians (*Corynactis californica* and *Plumularia* sp.), bryozoans (*Eurystomella bilabiata* and others), polychaetes (*Spirorbis* sp.), gastropods (*Petaloconchus montereyensis*), and ascidians (*Aplidium californicum* and *Distalpia occidentalis*). Often individuals of *O. carmela* were overgrowing other encrusting organisms, especially the bryozoan *E. bilabiata* (Fig. 2 B). Surprisingly, *O. carmela* has not been found in mid or low zones, although thorough searches down to the low zone were made at all the sites where it was found in the high zone.

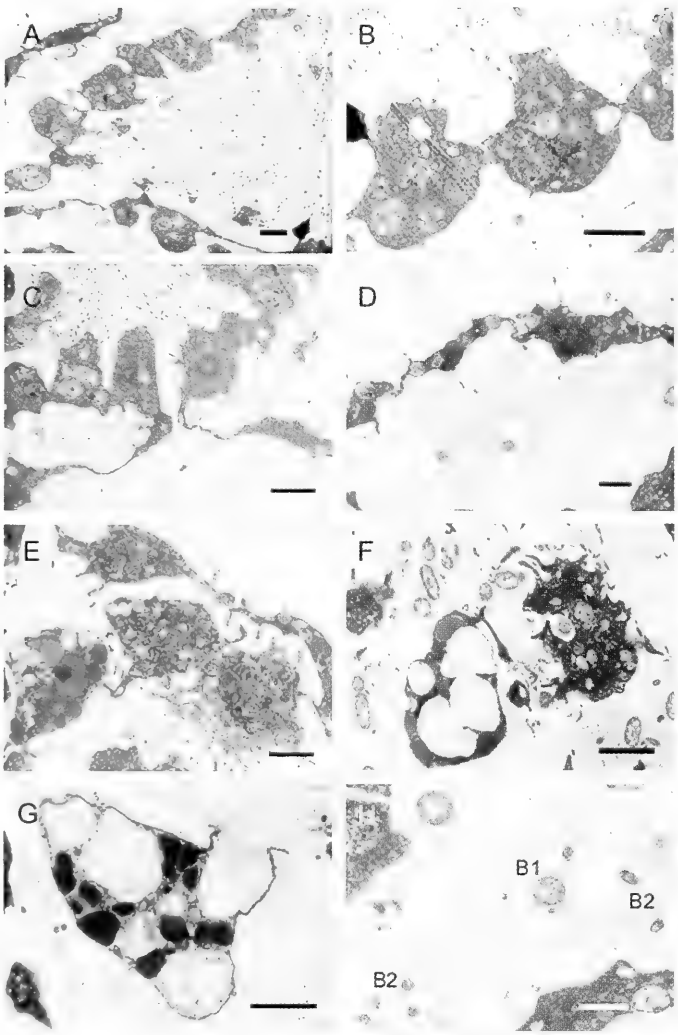

FIGURE 4. Cytology of *Oscarella carmela* sp. nov. (TEM). (A) section through a choanocyte chamber; (B) choanocytes; (C) prosopyle of a choanocyte chamber showing choanocytes (top) and endopinacocytes (bottom); (D) pinacocytes; (E) type 1 cell with inclusions (left), two archaeocytes (middle and right), and the loose junction between two pinacocytes (top right); F, type 2 cell with inclusions ("spherulous-vacuolar cell", left) and archaeocyte phagocytizing a bacterium (right); (G) type 2 cell with inclusions ("spherulous-vacuolar cell"); (H) endobiont bacteria types 1 (B1) and 2 (B2). Scale bars: A–G = 2 μm; H = 1 μm.

Specimens of *O. carmela* often grew profusely in aquariums and sea tables of the Long Marine Laboratory–Seymour Marine Discovery Center complex of the University of California, Santa Cruz, covering submerged rocks and plastic trays right up to the edge of the water line (Fig. 2E). In quiet aquarium water, the sponges developed conspicuous folds with bulging excurrent canals converging on large oscula (Fig. 2F). Asteroids (*Asterina miniata, Dermasterias imbricata, Pisaster ochraceus*) and abalones *(Haliotis rufescens*) in some of the sea tables and aquariums did not appear to disturb the sponges.

Specimens of *O. carmela* have been noticed in several of the exhibits of the Monterey Bay

Aquarium for many years, especially in the "Crevice Dwellers" tank, where they are particularly abundant during the spring (Veronica Franklin, pers. commun.). They grow on the artificial rock backing of the tank and on the shells of rock scallops (*Crassodoma gigantea*). The specimens have only been seen in tanks containing local biota and not in tanks with exotic species (e.g., the tank with Mediterranean cuttlefish); all seawater is filtered both before and after it leaves tanks with exotic species.

Distribution.— *Oscarella carmela* occurs in aquariums and sea tables of the Long Marine Laboratory–Seymour Marine Discovery Center complex, the Monterey Bay Aquarium, and in an aquarium of the Bodega Marine Laboratory of the University of California, Davis, approximately 150 km north of Monterey Bay (Scott Nichols, pers. commun.). However, specimens of *O. carmela* are not ubiquitous in marine laboratories and public aquariums along the California coast. For instance, it was not found in any of the aquarium tanks in the Steinhart Aquarium of the California Academy of Sciences in San Francisco nor in aquariums at the Long Beach Aquarium in southern California. Moreover, it has not been found in any of the tanks with running seawater at Stanford University's Hopkins Marine Station, which is adjacent to and receives all its seawater from the Monterey Bay Aquarium.

Specimens of *O. carmela* were first found in the field by JSP at Carmel Point on September 2002 and sampled on November 2002. The sponges were on boulders in high intertidal pools directly west of the intersection of Scenic Road and Ocean View Avenue, and to the north of the "Sunburst" house on the ocean side of Scenic Road (see: *http://limpets.noaa.gov/monitoring/rockyIntertidal/sites/mbnms/carmelpoint.html*). The site at Carmel Point was visited again on January 2003, several weeks after unusually heavy storms. Many of the boulders in the high tide pools had been disturbed and rearranged, but thin colonies of *O. carmela* were found on the undersurfaces of some of them. On April 2003, a thorough search of the boulders was made throughout the area from the high zone, through the mid zone dominated by the alga *Mazzaella flaccida,* to well into the low zone dominated by surfgrass (*Phyllospadix* spp.). Three out of about 20 boulders at the original high-zone site had specimens of *O. carmela* growing on their undersurfaces. Only one small colony of *O. carmela* was found elsewhere, on the underside of a boulder in a high-zone shallow tide pool west of the "Sunburst" house, approximately 30 m southwest of the area where the first individuals were seen.

The site at the NW corner of Carmel Point was examined six other times: May, August, and December 2003, and January, February, and April 2004. Specimens were found under boulders in the original pools on all these dates, and when looked for again on August 2003 and January 2004, small individuals at the site west of the "Sunburst" house were also found.

Between April 2003 and May 2004, thorough searches were made of 12 additional intertidal sites during low tides around Carmel Bay and the Monterey Peninsula (Fig. 1). One or more specimens were found at three of these sites: (1) Whaler's Cove at Point Lobos, rip-rap boulders adjacent to the boat launch, February and April 2004, three colonies total; (2) Lovers Point Beach, Pacific Grove, east of the beach at base of cliff below the intersection of Grand Avenue and Ocean View Boulevard, 6 February, 15 February, and 7 March 2004 (three colonies total), but not found on 21 February 2004, nor in boulder field just SE of Lovers Point on 7 March 2004; (3) Hopkins Marine Station, directly north of shop building, March, May, and July 2004, four colonies; but none found during thorough searches on November 2002 and May 2003. At all of these sites, specimens of *O. carmela* were found on the undersurfaces of partially submerged boulders in high-zone pools, similar to where they were found at Carmel Point. Similar habitats occurred at the other eight sites examined, but no individuals of *O. carmela* were found. Particular attention was given to the area under and around the Monterey Bay Aquarium, including the outflow channels from the facility,

which would likely carry propagules from the exhibit tanks.

In addition to the Monterey Peninsula area, six sites with boulders in the high zone between Monterey and San Francisco to the north were examined without finding specimens of *O. carmela.* These sites were: (1) James V. Fitzgerald Marine Reserve, Moss Beach; (2) Pigeon Point, south side; (3) Point Año Nuevo, south side; (4) Terrace Point adjacent to the outflow from the Long Marine Laboratory–Seymour Marine Discovery Center facilities; (5) Point Santa Cruz (Lighthouse Point), east side; (6) Elkhorn Slough, northwest of Highway 1 bridge. Although the type locality of another slime sponge, *Halisarca sacra* de Laubenfels, 1930, was in Elkhorn Slough close to this site, neither it nor *O. carmela* was found there.

On the other hand, after seeing specimens of *O. carmela* in aquariums at Long Marine Laboratory, J.H.R. Goddard (pers. commun.) told us he had seen it at Cape Arago, Oregon, where it was distinctly different from specimens of *Halisarca* found there (see below). A photograph he shared with us, taken at North Cove, Cape Arago on 22 May 1985, shows a thin, orange-tan specimen, which appears to be identical with specimens of *O. carmela* around the Monterey Peninsula. In addition, W.C. Austin informed us that he found a slime sponge with spherical choanocyte chambers characteristic of *Oscarella*, and distinct from *Halisarca* sp., in the Vancouver Aquarium in British Columbia (pers. commun., 1 June 2004).

Etymology.— The name carmela derives from the site where this species was first found in the field, Carmel Bay in Central California.

Discussion

Comparison of fixation methods.— Proper fixation is important for the identification of *Oscarella* species. These sponges are very sensitive, and a delay of only a few minutes before placing them in fixative may make them stop filtering, start contracting, and their tissues and cells loose their normal aspect. Bouin's solution, 4% formalin or 70% ethanol preserve canals and choanocyte chambers well enough to allow their recognition as belonging to *Oscarella* and not to, for instance, *Halisarca* (see below). However, these solutions rarely preserve the natural shape of chambers and cells or allow observation of cell contents, which are important taxonomic characters at the species level. We suggest that the best way to fix these sponges for both semithin (LM) and ultrathin sections (TEM) is to put small pieces of the sponge into freshly prepared 2.5% glutaraldehyde in seawater immediately after collection, preferably while still underwater. In the laboratory, the fixative should be changed to ensure it has the desired concentration. After 24 hrs, the pieces should be post-fixed with osmium tetroxide and then dehydrated until the ethanol concentration is 70%–100%. Following this treatment, they can be stored in ethanol for long periods before making sections for observation in LM or TEM. Boury-Esnault et al. (1984) compared the results of fixation in four different fixatives for TEM and SEM (scanning electron microscopy) in *Oscarella lobularis* and *Corticium candelabrum*, with varying osmolarity (1100 –1440 mosm) and different concentrations of glutaraldehyde (0–3.0 %), seawater, cacodylate buffer (0–0.4 M), and NaCl (0–7%). They concluded that their fixative C (2.5% glutaraldehyde in 0.4 M cacodylate buffer, pH 7.4, and seawater 4 vol.: 5 vol., 1120 mosm; rinse in seawater 1100 mosm) was the best fixative for homosclerophorid sponges.

Taxonomy of *Oscarella*.— The identification of *Oscarella* at the species level is difficult. The species are homogeneous in most of the few taxonomic characters available: encrusting shape, sylleibid aquiferous system organization, choanocyte chambers spherical-ovoid with 30–60 μm in diameter, cinctoblastula larvae, thin ectosome, etc. (Boury-Esnault et al. 1984, 1992; Muricy et al. 1996; Muricy and Diaz 2002). The differences among species are mostly in external traits: color,

consistency, and aspect of the surface. These characters, however, must be used with care, inasmuch as they can vary within a single species. Specimens of *Oscarella lobularis* (Schmidt, 1862) and *O. tuberculata* (Schmidt, 1868) from the Mediterranean, for example, may appear in several different colors: white, yellow, green, red, violet, and blue. However, each species is constant and unique in its cell contents (Boury-Esnault et al. 1992). Other species appear in only a single color such as *O. viridis* Muricy et al., 1996 (green) and *O. microlobata* Muricy et al., 1996 (brown). The consistency seems to be more constant within species, but it is also more subjective to describe. Finally, the aspect of the surface (smooth, microlobate) is also helpful, but one cannot separate all species on that basis alone. *Oscarella carmela* varies from light brown to tan or dull orange color, and from a smooth to microlobate surface; when out of the water, especially, the microlobes contract and the surface becomes smooth. The new species is similar in color and surface aspect only to *Oscarella microlobata*.

Because species of *Oscarella* have no skeleton, and histological characters are homogeneous among different species, less usual characters, such as the types of cells with inclusions present, are critical for species identification. Cells with inclusions are special sponge cells with different cytoplasmic inclusions, most of which have unknown functions (e.g., Simpson 1984; Muricy and Diaz 2002). They are abundant and diverse in species of *Oscarella*, and in the Mediterranean each species has a particular set of cells with inclusions that are useful characters for species identification (Muricy et al. 1996). It is, therefore, important that the specimens are fixed in glutaraldehyde, so they can be observed under TEM to identify cells with inclusions accurately. Cytological characters are also useful for the identification of other sponges without skeleton, such as *Halisarca* (*cf.* Vacelet and Donadey 1987). Molecular methods (e.g., allozyme electrophoresis, DNA sequencing) may also help in the definition of species boundaries in *Oscarella*.

The new species differs from *Oscarella microlobata* and all other Mediterranean *Oscarella* species in its cell contents, which are simple, with only two kinds of cells with inclusions: spherulous cells with two different inclusions, osmiophilic and filamentous, and vacuolar-spherulous cells (Fig. 4E-G). In contrast, *O. microlobata* has one type of vacuolar cells and three types of cells with inclusions, all different from those of *O. carmela*: spherulous cells with granular inclusions, spherulous cells with paracrystalline inclusions, and single-inclusion cells (Muricy et al. 1996). Besides being green, *O. viridis* differs from *O. carmela* by having two exclusive types of spherulous cells, called crescent-shaped cells and microgranular inclusions cells (Muricy et al. 1996). *Oscarella imperialis* is yellowish-white and has four types of cells with inclusions, two of which with different paracrystalline inclusions and two with large vacuoles with clear or osmiophiolic inclusions (Muricy et al. 1996); none of these cell types occur in *O. carmela*. *Oscarella tuberculata* is distinguished by the large groups of turgid vacuolar cells that fill most of the choanosome, and *O. lobularis* has two types of vacuolar cells, one of which is exclusive, and no spherulous cells (Boury-Esnault et al. 1992). The new species, therefore, has a set of cells with inclusions clearly distinct from those of all Mediterranean species of the genus, which are the only other species of *Oscarella* studied at TEM so far. *Oscarella carmela* is distinct also in its intertidal habitat: all known Mediterranean species of *Oscarella* occur in caves or in subtidal rocky shores (Boury-Esnault et al. 1992; Muricy et al. 1996).

Two other species of *Oscarella* were recently described from the Indo-Pacific (Bergquist and Kelly 2004). These specimens were fixed in 70% ethanol, and no attempt was made to characterize their cell composition. However, it is possible to distinguish both from the new species by their external characters: *Oscarella stillans* Bergquist and Kelly, 2004 forms a series of fused tubes up to 3.5 cm long, some with solid branches, and it is dark honey yellow in color. It also has a characteristically high collagen deposition in the mesohyl, giving it a collagenous consistency.

Oscarella nigraviolacea Bergquist and Kelly, 2004 differs from the new species by its dark violet, almost black color, and the oscules situated on top of papillae. According to Bergquist and Kelly (2004), other possibly valid species of *Oscarella* are *O. tenuis* Hentschel, 1909, *O. membranacea* Hentschel, 1909 (both from south Australia), and *O. ochreacea* Bergquist and Kelly, 2004 (*nomen novum* for *O. lobularis* sensu Vacelet et al. 1976) from Madagascar. However, these species must be better characterized before meaningful comparisons can be made.

Distinction from *Halisarca* and other sponges without skeletons.— With the finding of *Oscarella* along the California coast, there is now a need to distinguish *Halisarca* sp. from *O. carmela*, inasmuch as they belong to two superficially similar but unrelated sponge families. *Halisarca* sp. is the only tan colored sponge in the current standard keys for sponges in central California (Hartman 1975) and the northeast Pacific (Kozloff 1974) that has neither a collagen nor spicule skeleton. In these keys *Oscarella* would not be distinguished from *Halisarca*. The complete absence of a skeleton is also shared with *Chondrosia* Nardo, 1833, another common sponge genus, and three less common genera, *Hexadella* Topsent, 1896, *Bajalus* Lendenfeld, 1885, and *Pseudocorticium* Boury-Esnault et al., 1995. However, among these genera, only *Hexadella* is recorded for the West Coast of North America, and it is distinguished from *Halisarca sacra* and *O. carmela* by its bright yellow color when live (Kozloff 1996).

These genera can also be distinguished through examination of transverse sections to observe the shape and size of the canals, choanocyte chambers, and larvae. In *Oscarella*, the choanocyte chambers are ovoid to spherical, 30–60 μm in diameter, eurypilous, and arranged in a sylleibid organization (the chambers are regularly arranged around the exhalant canals); the larvae of *Oscarella* are incubated, hollow cinctoblastulae (Fig. 3H). Such larvae are typical of the family Plakinidae (including *Oscarella* and *Pseudocorticium*; Diaz and van Soest 1994; Muricy and Diaz 2002). In *Halisarca*, the choanocyte chambers are elongate, up to 280 μm long, tubular, ramified, with a large exhalant opening, and arranged in a leuconoid organization. The larvae are incubated, solid parenchymellae. In *Chondrosia*, the choanocyte chambers are spherical, 10–30 μm in diameter, diplodal, and arranged in a leuconoid organization. There is always a thick, easily recognizable collagenous cortex, absent in the other genera. *Hexadella* has a distinct collagenous ectosome, which provides some mechanical support in the absence of a skeleton. The choanosme is soft, with eurypilous, sac-shaped choanocyte chambers, approximately 60–80 μm in diameter. Its spherulous cells are typical of the Verongida (Bergquist and Cook 2002).

There are also differences in external morphology among these genera, but such traits are less reliable for identification: *Chondrosia* has a firm, cartilaginous consistency, and a smooth surface. Both *Oscarella* and *Halisarca* have a soft and fragile consistency, but *Halisarca* has an even, smooth surface in which superficial canals can be seen sometimes. The lobulated surfaces of *Oscarella* and *Hexadella* do not have superficial canals, although prominent excurrent canals can often be seen below the surface (Fig. 2F). Species of these genera vary in thickness. Those of *Oscarella* and *Hexadella* are usually thicker (5–30 mm thick) than species of *Halisarca* (usually less than 5 mm). On the other hand, our specimens of *O. carmela* were usually only 1 mm thick or less, and rarely thicker than 5 mm even when growing in quiet water in the laboratory. In contrast, W. C. Austin (unpublished manuscript, 2004) reports that specimens of *Halisarca* growing in quiet waters in British Columbia can be up to 1 cm thick (see also Goddard [1984, 2001]) for photographs of thick specimens of *Halisarca* in Oregon).

Status of *Halisarca* on the West Coast of the United States and Canada.— The only described species of *Halisarca* in the northeastern Pacific, *H. sacra*, is based on specimens collected by Ed Ricketts in 1929 from rocks resting on a sheltered mud flat just within the former mouth of Elkhorn Slough, Monterey Bay. However, there has been some question about the validity of the

species (Ristau 1977); Hartman (1975) changed its designation from *H. sacra* de Laubenfels, 1930 in Hartman and Smith (1954) to *Halisarca* sp. without comment. Smecher (2004) includes *H. sacra* in his website but considers it to be synonymous with *Halisarca dujardini* Johnston, 1842. He also reports that specimens are in the British Columbia Provincial Museum (Smecher 2004), but upon inquiry he replied that the museum does not have the facilities to do proper sections (C. Smecher, pers. commun.). Similarly, Austin (1985) includes *Halisarca sacra* in his checklist, as does Austin et al. (1999–2001) on their website which includes a photo, but the latter with the caveat that it may be synonymous with *H. dujardini* Johnson 1842. Austin (unpublished manuscript, 2004) describes specimens of *Halisarca* collected from southeast Alaska, British Columbia, and northwest Washington and sectioned to reveal the tubular choanocyte chambers, and suggests that they are synonymous with *H. sacra* de Laubenfels, 1930. Goddard (1981) acknowledged P. Bergquist and W. Hartman for identification from prepared histological sections of *Halisarca* from Oregon, but they refrained from giving a specific name.

There are no confirmed records of *Halisarca* in California except for the original collections in Elkhorn Slough, the type locality of *H. sacra* de Laubenfels, 1930 (de Laubenfels, 1932) (types in the National Museum of Natural History, K. Rützler, pers. commun., 2004). MacGinitie (1935) mentions the species in his classic monograph on Elkhorn Slough, but apparently only on the basis of the original description; it is not mentioned at all in MacGinitie and MacGinitie (1949). In their survey of Elkhorn Slough, Nybakken et al. (1977) list *H. sacra* only because it was mentioned in MacGinitie (1935), and they did not find it themselves (J. Nybakken, pers. commun., 2004). Similarly, Ricketts and Calvin (1939) reported that *H. sacra* is known to occur in Elkhorn Slough, apparently on the basis of the original collection and description, and that report is retained unchanged in later editions of their book (Ricketts et al. 1985). The genus is not included in Bakus and Abbott's (1980) account of Californian intertidal sponges, Thompson et al.'s (1985) list of sponges from San Diego, California, or Bakus and Green's (1987) account of sponges in the Southern California Bight.

On the other hand, the nudibranch *Hallaxa chani*, which apparently feeds exclusively on *Halisarca* sp., (Goddard 1981, 1984, 2001), ranges from southeast Alaska to central California (Gosliner and Johnson 1994) and into the Channel Islands (Goddard, pers. commun., 2004). Consequently, *Halisarca* sp. probably also occurs in California but, if so, it would likely be seen rarely because it is so obscure and perhaps kept at low densities by predation by *H. chani* and a second nudibranch predator, *Cadlina modesta* (Goddard 1984, 2001). The Santa Barbara Museum of Natural History has two ethanol-preserved specimens collected from southern California that were identified by R. Given as *H. sacra* (SBMNH 353403, Moray Reef, Corona del Mar, Orange County, 50 ft, 26 March 1958; SBMNH 353402, Scorpion Anchorage, Santa Cruz Island, Santa Barbara County, 30–40 ft, 24 March 1963). These specimens were examined by one of us (JSP). Although histological sections were not made to reveal the choanocyte chambers, thick sections indicated that the specimens are definitely not *O. carmela,* based on thickness, surface texture, distinct stiff ectosome, thick collenchymatous choanosome, and large excurrent canals. They almost certainly are specimens of *Halisarca,* or perhaps of *Hexadella.*

Halisarca sp. is included in species lists prepared in the early 1970s during undergraduate student surveys at Point Año Nuevo and Pigeon Point, north of Monterey Bay (Pearse, 1980; unpublished). However, no vouchers were retained and because the keys used then (a draft of Hartman's 1975 keys) would not distinguish between *Halisarca* sp. and *O. carmela,* the identity of those records is uncertain. Similarly, using available keys, JSP identified skeleton-less sponges as *Halisarca* that were collected in the early 1970s at the same site at Carmel Point where *O. carmela* is now found (unpubl. obs.). It is likely that those specimens were *O. carmela,* which would sug-

gest that the species has been present at the type locality at least since the early 1970s. In support of this continuous presence, M. C. Diaz, who identified *O. carmela* growing at Long Marine Laboratory, noted it to be present at Carmel Point during a field trip in 1993 (K. Wasson, pers. commun., 2004). On the other hand, an undergraduate student survey of the sponges at Carmel Point in 1993 did not list *O. carmela* (or *Halisarca* sp.) (JSP, unpublished list), so it is rare and/or easily overlooked even at the type locality. Because of its slimy, non-sponge appearance, which could be confused with encrusting ascidians, and its unusual habitat in the high intertidal, it would not be difficult for students to miss.

Distribution in the field and aquariums.— The spatial distribution of *O. carmela* is puzzling. Despite extensive searching in the vicinity of the Monterey Peninsula of central California, small, scattered individuals were found in only a few localities in the high intertidal zone. It was not abundant anywhere, and there was no evident pattern in the four sites where it was found in this study. On the other hand, it is difficult to find in the field, even when a search image is established. Thin sheets of encrusting ascidians (e.g., *Aplidium* spp., *Diplosoma listerianum*) and sponges (e.g., *Zygherpe hyaloderma, Astylinifer arndti*) were misidentified as *O. carmela* in the field by JSP; only inspection of specimens with a microscope revealed the error. Nonetheless, once noticed, it is quite conspicuous and hard to miss. Outstanding intertidal biologists (e.g., Ed Ricketts, Don Abbott) collected specimens in the intertidal of the Monterey Peninsula for most of the 20th century. Inasmuch as *O. carmela* is rather unattractive and usually occurs as small, slimy colonies adhering to large boulders, perhaps after de Laubenfels'1932 monograph was published, experienced intertidal biologists simply field identified it as *Halisarca sacra* and then went on to other things. Moreover, they could have been discouraged because of the difficulty in identifying slimy sponges. For example, in reference to *H. sacra*, Ricketts and Calvin (1939:176) wrote: "Since there are various additional species not mentioned, which, on the basis of field characters alone, could be confused with the above, and with previously treated species, the value of careful laboratory work should be kept in mind."

Another possibility is that *Oscarella carmela* normally occurs in deeper water, or in caves and hard-to-reach places, as do other species of *Oscarella* (Muricy and Diaz 2002). After all, it almost always occurs submerged in pools in the intertidal and does well in dimly lit aquariums. However, since being alerted about its appearance, two observant diving biologists (Anthony Draeger and Scott Nichols) have searched for it subtidally on the Monterey Peninsula without success.

Although rarely encountered in the field, and then only as small individuals, *Oscarella carmela* often thrives in aquariums, exhibit tanks, and sea tables in laboratories and public aquariums. This difference in abundance between the field and on-shore facilities indicates that there are factors operating to limit the sponge's establishment and growth in the field. Perhaps it is preyed upon heavily in the field by some unknown predator, which severely limits its growth subtidally and leads to it occurring mainly as small refuge populations under boulders in high intertidal pools. That appears to be the case for *Halisarca* sp. in the eastern Pacific (Goddard 1981, 1984, 2001), which is also rarely encountered, especially in California.

The source of the specimens of *Oscarella carmela* in aquariums continues to be unknown. It has been found in three on-shore facilities: (1) Long Marine Laboratory–Seymour Marine Discovery Center complex, (2) Monterey Bay Aquarium, and (3) Bodega Marine Laboratory. These are completely separate facilities, and it is unlikely that material was transferred among them. Moreover, Hopkins Marine Station receives all its running seawater from the Monterey Bay Aquarium, and *O. carmela* has not been found in any of the aquariums there. Furthermore, the sponge has not been found in the intertidal near two of the facilities when those habitats were searched. Consequently, the source is probably not via seawater being brought into the facilities.

Rather, small specimens probably are brought into the facilities on rocks and other material collected from the intertidal. There is also no evidence that the species has escaped from the facilities to colonize nearby intertidal areas.

Temporal dynamics.— It is not known whether the colonies of *Oscarella carmela* are new to Carmel Point and other sites around the Monterey Peninsula, signaling an environmental change, or were simply overlooked in the past. If specimens keyed as *Halisarca* from the same area at Carmel Point in the early 1970s by JSP were, in fact, *O. carmela*, then they have probably been there for a long time. They almost certainly were present since 1993, when M.C. Diaz saw them there (K. Wasson, pers. commun.).

After specimens of *Oscarella carmela* were recognized in high zone pools at Carmel Point in September 2002 by JSP, largely because they looked similar to specimens at Long Marine Laboratory, they were found there on each of nine subsequent visits, extending from November 2002 to April 2004. Specific individuals were not followed, mainly because the boulders were similar in appearance and appeared to be rearranged between visits by storms. In January 2003, after a major winter storm, the specimens were noticeably thin, and in the spring (April and May) they appeared to be particularly robust, as is the case for many intertidal organisms of the northeast Pacific (Foster et al. 1988). The abundance of *O. carmela* in the Monterey Bay Aquarium was somewhat seasonal too, with an increase in spring months and a die-off during winter (Veronica Franklin, pers. commun.). A similar pattern is found in calcareous sponges in Rio de Janeiro state, Brazil, belonging to the genera *Clathrina* and *Paraleucilla* (Michelle Klautau, pers. commun., 2003).

Indigenous or invasive?.— *Oscarella carmela* has been known for a long time in labs and local public aquariums before being noticed in the field, a pattern suggestive of an invasion. If this sponge were similar to any described species of *Oscarella* from other region, it could be concluded that it has invaded central California recently. Instead, the species has proved to be new, and it now seems likely that it is reasonably widespread at least between central California and British Columbia, thus suggesting that it is indigenous. This conclusion is consistent with the finding that nearly all introduced marine species in California are found in estuaries and harbors, and only a subset of these occur on the open coast (Wasson et. al., in press). Specimens of *O. carmela* have not been found in estuaries of central California that are populated by a high number of introduced species (San Francisco Bay, Andy Cohen and Jim Carlton, pers. commun.; Elkhorn Slough, Wasson et al., in press).

On the other hand, the taxonomy of the genus *Oscarella* is so poorly known worldwide that it is nearly impossible to know if it is really indigenous or introduced. Although we believe that there is a high probability that the new species is indigenous of this area, we cannot completely discard the possibility of an invasion from an unknown population of an undescribed species that originated elsewhere. There are no previous records of the genus *Oscarella* along the Pacific coast of North America, but this may be due to rarity and difficulty in identifying these species. The temporal dynamics of *O. carmela* shows high seasonal and pluri-annual fluctuations. Therefore, it is likely that, in this case, there has been an increase of abundance at a few localities of a previously rare, resident species, rather than an invasion.

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A Phylogenetic Analysis of the Aegiridae Fischer, 1883 (Mollusca, Nudibranchia, Phanerobranchia) with Descriptions of Eight New Species and a Reassessment of Phanerobranch Relationships

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The phylogenetic relationships among the Aegiridae are examined based upon morphological characters of all presently described species and eight new species. The Aegiridae are a monophyletic clade of phanerobranch dorids, a paraphyletic group previously united by the absence of a retractable dorsal gill, which is a pleisomorphic character. There are three traditionally recognized genera within the Aegiridae, *Aegires* Loven, 1844, *Notodoris* Bergh, 1875 and *Triopella* Sars, 1878. Most species of each genus were examined anatomically and some previously undescribed characters were included in the analysis such as details of the central nervous system. Published literature descriptions were utilized in cases where no specimens were available for examination. From the literature review and anatomical examinations, sixty-four characters were considered. These characters were polarized using *Bathydoris* and the type species of several phanerobranch genera. Additionally, four cryptobranch dorids were included in the analysis for comparative purposes. The phylogeny obtained supports both the monophyly of Aegiridae and that *Notodoris* is a monophyletic clade nested within *Aegires*. *Triopella incisa*, the type species of a monotypic genus, is nested within *Aegires* and is the sister species of *Aegires sublaevis*. This phylogeny necessitates inclusion of *Notodoris* and *Triopella* as junior synonyms of *Aegires* to preserve the monophyly of *Aegires*. This also renders *Aegires citrinus* Pruvot-Fol, 1930 as a junior homonym of *Aegires citrinus* (Bergh, 1875). The new name *Aegires pruvotfolae* is given to this former species. The following are new species of *Aegires*: *A. exeches* sp. nov., *A. flores* sp. nov., *A. hapsis* sp. nov., *A. incusus* sp. nov., *A. lemoncello* sp. nov., *A. malinus* sp. nov., *A. ninguis* sp. nov. and *A. petalis* sp. nov. All these new taxa are found in the Indo-Pacific except *A. ninguis*, which is found in temperate South Africa. Unique combinations of morphological characters distinguish these as new species of *Aegires*.

The present phylogeny supports the notion that the Phanerobranchia represents a paraphyletic group. The Suctoria are the sister group to the Cryptobranchia. Aegiridae is the sister group to Cryptobranchia plus Suctoria. Polyceratidae is the sister group to Cryptobranchia plus Suctoria plus *Aegires*. *Hexabranchus* is basally situated to all of these other taxa but is more derived than *Bathydoris*.

Aegiridae Fischer (1883) is one of the families of the traditional group Phanerobranchia (Fischer 1880–1887). The classification of the family Aegiridae (= Notodorididae Eliot, 1910) has an interesting, although convoluted history and is presented in detail below and summarized in

Table 1 (see Appendix). According to the most recently published classification of the Aegiretidae [*sic*] (Rudman and Willan 1998) there are only two recognized genera within the group: *Aegires* Lovén, 1844 and *Notodoris* Bergh, 1875. However, *Triopella* Sars, 1878 is also a genus that has been overlooked by most researchers.

The primary character that unites all Phanerobranchia, including Aegiridae, is the presence of a non-retractable dorsal gill. As a result of having an unprotected gill, these animals have developed protective appendages for the gill leaves. This adaptation provides some important information for phylogenetic analyses, which is discussed in detail in a later section. Thompson (1976) described the protective appendage in his characterization of the Superfamily Anadoridoidea (Odhner's [1939]), Suborder Anadoridacea. Fischer et al. (1968) were the first to equate Anadoridacea with the Phanerobranchia Fischer, 1883. The Phanerobranchia are now thought to be paraphyletic (Valdés 2002).

Historically, the Suborder Anadoidacea was divided into two tribes (Bergh 1890), the Suctoria and Non-suctoria. Aegiridae is one of the three currently recognized families within the tribe Non-suctoria along with Triophidae Odhner, 1941 and Polyceratidae Alder and Hancock, 1855 (amended from the original authors' spelling) (Rudman 1998). While these three families have a widely variable external anatomy there are also some similarities. These include the anus and the gill situated medio-dorsally, a well-developed radula usually lacking a rachidian tooth, the edge of the mantle more or less reduced, and a contractile gill that is not retractile. Some of the internal differences between the families include genital organs that may have small hooks on the vas deferens or be unarmed and either a smooth jaw or a jaw having rods (Fischer et al. 1968).

The characters that unite Aegiridae (as noted first by Thiele 1931, although he had called the Family Notodoridinae) include: "a hard body with calcareous spicules, gills that have a separate integumental fold, rhinophores that retract and in most cases, are not lamellate, radula without a rachidian tooth and all lateral teeth hook- or arch-shaped."

Several of the species of both *Aegires* and *Notodoris* were originally described in very abbreviated terms, or based on single specimens. Some entire organ systems were never described either initially or by subsequent workers. In the present study, specimens of each species were examined when available and when not available, all published literature was reviewed. Anatomical details are described for all known species of each genus, some of these details for the first time.

The present study provides an in-depth look at the Aegiridae and presents a phylogenetic analysis of the placement of this family within the Phanerobranch dorids (the Anadoridoidea). The name Phanerobranchia is the most widely used and recognized name, and it is used here instead of the synonymous Anadoridoidea.

Eight new species are described based on examination of material lodged at the California Academy of Sciences and the South African Museum.

History of Aegiridae Classification

Lovén (1844) introduced the new genus *Aegires* without designating a family affiliation. For the type species of his new genus, he selected *Polycera punctilucens* (D'Orbigny 1836–1842).

Alder and Hancock (1845–1855) labeled the first Suborder in their classification of the Nudibranchia, Anthobranchia. In the early years of the monograph (1845) they placed *Aegires* within Family #1, Doridídae, (Sub-Family Polycerinae), along with *Thecacera, Polycera* and *Idalia.* Later, in 1855, they proposed to use a classification originally suggested by Gray, which now named Family #2 the Doridídae, and which now included *Aegires* with *Doris, Goniodoris* and *Ceratosoma.*

Bergh (1875) introduced the new genus *Notodoris* and drew some anatomical features of the type species *Notodoris citrina*. However, he did not designate a familial association.

Sars (1878) described and drew the type species for his new genus *Triopella* (*incisa*). He mentions the radular similarities between *Triopella* and *Aegirus* in the discussion of the new species.

Fischer (1880–1887) divided the Nudibranchia into 5 suborders: Anthobranchiata, Inferobranchiata, Polybranchiata, Pellibranchiata and Parasita. He further divided the Anthobranchiata into Aglossa and Glossophora. The Aglossa had one family, Doridopsidae, while the Glossophora were subdivided into three groups: the Cryptobranchiata (with one family, Dorididae), the Phanerobranchiata (Family Polyceridae) and the Abranchiata (Family Heterodorididae). Fischer, noting that *Triopella* and *Aegires* (which, like Sars, he spelled *Aegirus*) were closely related, placed both these genera in the Phanerobranchiata (Family Polyceridae) with no mention of *Notodoris*. Fischer did acknowledge that his Polyceridae corresponded to Bergh's "Doris phanerobranchs", so although Fischer left out *Notodoris* he was evidently aware of Bergh's 1875 publication. Fischer further separated the Polyceridae into three sub-families, Acanthodoridinae, Polycerinae and Aegirinae.

Bergh (1890) acknowledged Fischer's group Phanerobranchiata when he placed his two newly described species, *Plocamopherus amboinensis* Bergh, 1890 and *Plocamopherus indicus* Bergh 1890 into the Subfamily Phanerobranchiata (Suborder Nudibranchiata Holohepatica, Family Doridídae).

Two years later, when Bergh described the systematics of the Nudibranchia (1892:141) he placed *Aegires*, *Notodoris* and *Triopella* within the Polyceridae (Subfamily Doridídae Phanerobranchiatae Non Suctoriae). He used the spelling *Aegires* not *Aegirus* as Fischer did in 1883. This may have been in recognition of the indexed generic names published in *Nomenclator Zoologicus* (Scudder 1882).

Eliot (1903) placed his newly described *Notodoris gardineri* within the Family Doridídae Phanerobranchiatae (his spelling). He described the Phanerobranchiatae as those dorids that have no dorsal cavity into which the branchia can be retracted. Eliot acknowledged Bergh's (1875) division of the Phanerobranchiata into the Goniodorididae (which possesses a buccal gizzard) and Polyceradae (no gizzard), but stated that a more "natural" division would be Polyceradae (having limaciform bodies, sometimes bearing appendages) and Pseudodorididae (flat dorid-like forms). Eliot also noted in his study that *Notodoris* is closely related to *Aegires* and the little known *Triopella* because all three had a hard consistency and had branchiae and rhinophores protected by tubercles.

Eliot (1910:65) in *A Monograph of British Nudibranchiate Mollusca*, Part 8, went on to establish the Family Notodorididae for *Notodoris*, *Aegires*, and *Triopella*. He united these genera based upon their simple, hook-shaped teeth, branchial valves and smooth rhinophores. Eliot did not reference Fischer's 1883 family name Aegiridae at this time.

However, thirteen years later, in their classification, Iredale and O'Donoghue (1923) also used the family name Aegiretidae for *Aegires, Notodoris* and *Triopella* but without providing a diagnosis for this group. Apparently these authors were aware that Aegiretidae (Aegiridae) was an older name than Notodorididae.

In 1926, Odhner recognized that the Family Notodorididae = Aegiretidae, Iredale and O'Donoghue, incorrectly attributing the name Aegiretidae to these authors (and maintaining the incorrect spelling of the family name). Odhner provided two distinguishing characters for Notodorididae (Phanerobranchia): "Radular teeth hooked, uniform and tentacles small, inconspicuous".

Risbec (1928) provided a diagnosis for the Family Aegiridés [*sic*] using the genus *Aegirus*

Lovén 1844 as his model. In this document he also provided a lengthy description of *A. leuckartii* Verany, 1853 and synonymized *A. albopunctatus* MacFarland, 1905 with this species. This synonymy was later questioned by Schmekel and Portmann as will be discussed later in the present paper.

Pruvot-Fol (1930) placed a new species she described as *Aegires citrinus* into the Family Aegiretidae, with this particular spelling.

The following year, Thiele's classification (1931) placed *Aegires, Notodoris* and *Triopella* within the Subfamily Notodoridinae (Stirps Doridacea (= Holohepatica) Family Polyceridae). Thiele's diagnosis of the Notodoridinae follows: "Body hard, with calcareous spicules; gills with a separate integumental fold; rhinophores retractile, in most cases not lamellate; radula without central plate, all lateral plates hook- or arch-shaped."

Odhner (1934) established a new genus *Anaegires* with *A. protectus* as the type species. However, this new genus was based upon characters that were later found by Wägele (1987) to be within the realm of intraspecific variation. Wägele justifiably synonymized *A. protectus* with *A. albus* Thiele, 1912. Odhner also commented that Iredale and O'Donoghue (1923) should not have changed the family name to Aegiretidae without justification. Odhner stated that *Notodoris* may be kept as the type genus of the Family and thus Eliot's family name Notodorididae is valid. He completely overlooked the fact that the name Aegiretidae (Aegiridae) was used twenty-seven years prior to Notodorididae.

Pruvot-Fol (1954) placed *Aegires* in Aegiretidae noting that Thiele (1931) erroneously called the subgroup Notodorididae when he grouped *Notodoris* and *Aegires* in the family Polyceradae. Pruvot-Fol correctly pointed out that *Aegires* Lovén, 1844 is an older name than *Notodoris* Bergh, 1875. In this paper, Pruvot-Fol also synonymized *Aegires hispidus* (*Polycera hispida* Hesse, 1872) and *A. leuckartii* Verany, 1853 with *A. punctilucens* (*Polycera* d'Orbigny, 1837). However, she did not mention Risbec's previous (1928, 1953) synonymy of *A. hispidus* and *A. leuckartii* with *Aegires albopunctatus*.

In 1966, MacFarland classified the Notodoridinae (*sic*) as a subfamily of Polyceridae.

Fischer et al. (1968) placed Aegiretidae into the Anadoridacea Odhner (1968) in the tribe nonsuctoria (one of two tribes first identified by Bergh [1892]). Aegiretidae were considered Family #2 of the Anadoridacea (Family 1 = Triophidae Odhner *nov* and Family 3 = Polyceridae Alder and Hancock 1845). Fischer et al. wrongly attributed the name Notodorididae to Odhner, 1926, when in fact Eliot first established this group in 1910.

Nordsieck (1972) established a new genus *Serigea* naming *Aegires* (*Serigea*) *sublaevis* as the type species. He presented the following brief diagnosis of *Serigea*: "Features like *Aegires*, but without tubercles (papillae); rhinophore sheaths low, smooth. Only a few tubercles behind the rhinophores."

Notably, Nordsieck did not mention *Notodoris* in his manuscript on European marine molluscs when he grouped *Aegires*, *Triopella* and *Serigea* nov. gen. within the Family Aegiretidae Fischer, 1883. This is most likely because there are no known *Notodoris* species found in European marine habitats. He did pronounce as Pruvot-Fol did in 1954, that Aegiretidae = Notodorididae Odhner, 1926. Nordsieck thus continued the incorrect attribution of the name Notodorididae to Odhner, 1926 and the incorrect spelling of the family name.

Thompson (1976) changed the name Anadoridacea to Anadoridoidea, in which he included the Family Notodorididae. Thompson listed only *Notodoris* and *Aegires* as the genera in this family. He did not cite the authors of any family names. (see Valdés 2002 for a discussion of the Family name Anadoridacea).

Schmekel and Portmann (1982) used Thompson's name Anadoridoidea but erroneously attrib-

uted the name to Odhner (1959); a non-existent publication that was also omitted in their literature cited.

Gosliner and Behrens (1997) incorrectly attributed the name Notodorididae to Bergh (1897) in their description of the new *Notodoris serenae*. Bergh never used this name to categorize the new genus *Notodoris*. It wasn't until Eliot (1910) wrote the text for Part 8 of Alder and Hancock's monograph of the British nudibranchiate molluscs that this name was first used.

In the most recently published classification of Aegiretidae, Rudman (1998) placed *Aegires* and *Notodoris* in the Family Aegiretidae, Superfamily Anadoridoidea, suborder Doridina. *Triopella* was once again left out of the family and the incorrect spelling of the family name was continued. The correct spelling, Aegiridae is discussed in detail by Willan (2000). Table 1 (see Appendix) summarizes the historical classification of Aegiredae.

Material and Methods

Twenty-two species of Aegiridae were included in the analysis. This includes all known species of the recognized genera, *Aegires*, *Notodoris* and *Triopella* as well as eight additional, previously unidentified species of *Aegires*. In some cases, the complete published description of certain features of a species allowed the extraction of data from the literature, which was then verified by direct examination of a specimen when available. Type material and additional non-type material was obtained from the following sources: the California Academy of Sciences (CAS), the Los Angeles County Natural History Museum (LACM), the Natural History Museum of Norway, Oslo (D), the South African Museum (A) and the Museo National de Ciencias Naturales Madrid (MNCN). Specimens were drawn under a dissecting microscope using a camera lucida then dissected by dorsal incision. The internal anatomy was drawn as described and then examined either by compound or scanning electron microscope (SEM). External features were examined directly when specimens were available, by photographs, or by literature review. Special attention was given to the reproductive anatomy, the central nervous system and the circulatory system, as some of these features were infrequently (or cursorily) described in the literature. Dorsal tubercles of available specimens were drawn and examined by SEM. Table 2 (see Appendix) shows the list of character states derived from dissections and from the literature reviewed for the present study. Ten additional species were selected for outgroup comparison as discussed below.

Phylogenetic analytical methods

Phylogenetic analyses were performed using the program Phylogenetic Analysis Using Parsimony (PAUP) version 4.0 (Swofford 2001) using the heuristic algorithm (TBR branch swapping option). One hundred random start trees were obtained by stepwise addition. Bremer analyses were performed to estimate branch support (Bremer 1994). Characters were unordered and were polarized using *Bathydoris abyssorum* Bergh, 1884 as the outgroup. This type species was selected based on the analysis of the cryptobranch dorids by Valdés (2002), which showed that *Bathydoris* is sister to the dorids. Additionally, Wägele (1989a) and Wägele and Willan (2000) demonstrated that *Bathydoris* is the most basal member of the Anthobranchia and is the sister group to the rest of the dorid nudibranchs. *Polycera quadrilineata* (Müller 1776), *Okenia elegans* (Leuckart, 1828), *Onchidoris bilamellata* (Linnaeus, 1767), *Holoplocamus papposus* Odhner, 1926, *Diaphorodoris luteocinta* (Sars, 1870) and *Calycidoris guentheri* Abraham, 1876 were also tested as outgroup taxa in the analyses. These five additional genera are phanerobranchs and basally situated relative to the rest of the dorids. Four cryptobranch dorids were included in the analysis for comparative purposes. The genera were chosen from the most recent analysis of the crypto-

branch dorids (Valdés, 2002) and are the type species and represent the most basal taxa of their particular clade. Those genera are *Actinocyclus* Ehrenberg, 1831; *Conualevia* Collier and Farmer, 1964; *Hexabranchus* Ehrenberg, 1831 and *Mandelia* Valdés and Gosliner, 1999, which has been included in the Cryptobranchia in the most recent classification of the Doridina (Rudman 1998). The source of the information on the outgroup species included in the present analysis is shown in Table 3 (see Appendix). Synapomorphies were examined using MacClade and the character-trace option, using the majority rule tree from PAUP analyses.

Species Descriptions

Family Aegiridae Fischer, 1883

Genus *Aegires* Lovén, 1844

Type species: *Polycera punctilucens* d'Orbigny, 1837, by monotypy.
Type species: *Aegires albus* Thiele, 1912, by original designation.

Synonyms of *Aegires*: *Anaegires* Odhner, 1934:241, type species *Anaegires albus* Odhner, 1934 by monotypy; *Notodoris* Bergh, 1875:64, type species *Notodoris citrina* Bergh, 1875 by monotypy, syn. nov.; *Serigea* Nordsieck, 1972, type species *Serigea sublaevis* Nordsieck, 1972 by subsequent designation; *Triopella* Sars, 1878:310, type species *Triopella incisa* Sars, 1878 by monotypy, syn. nov.

Diagnosis.— Diagnoses of this genus have been provided by multiple authors: Lovén (1844), Schmekel and Portmann (1982), and Thompson and Brown (1984). A summary of these authors' diagnoses follows: The body is firm, with a reduced, indistinct mantle skirt. The dorsum is covered with numerous blunt, pedunculate dorsal tubercles. The rhinophores extend from cylindrical pallial sheaths that have tubercles around the rims. The gill is protected by tuberculate lobes. A median dorsal cuticular plate or jaw is present in the buccal mass. The radular teeth are simple, hamate and not bifid.

Aegires albopunctatus MacFarland, 1905

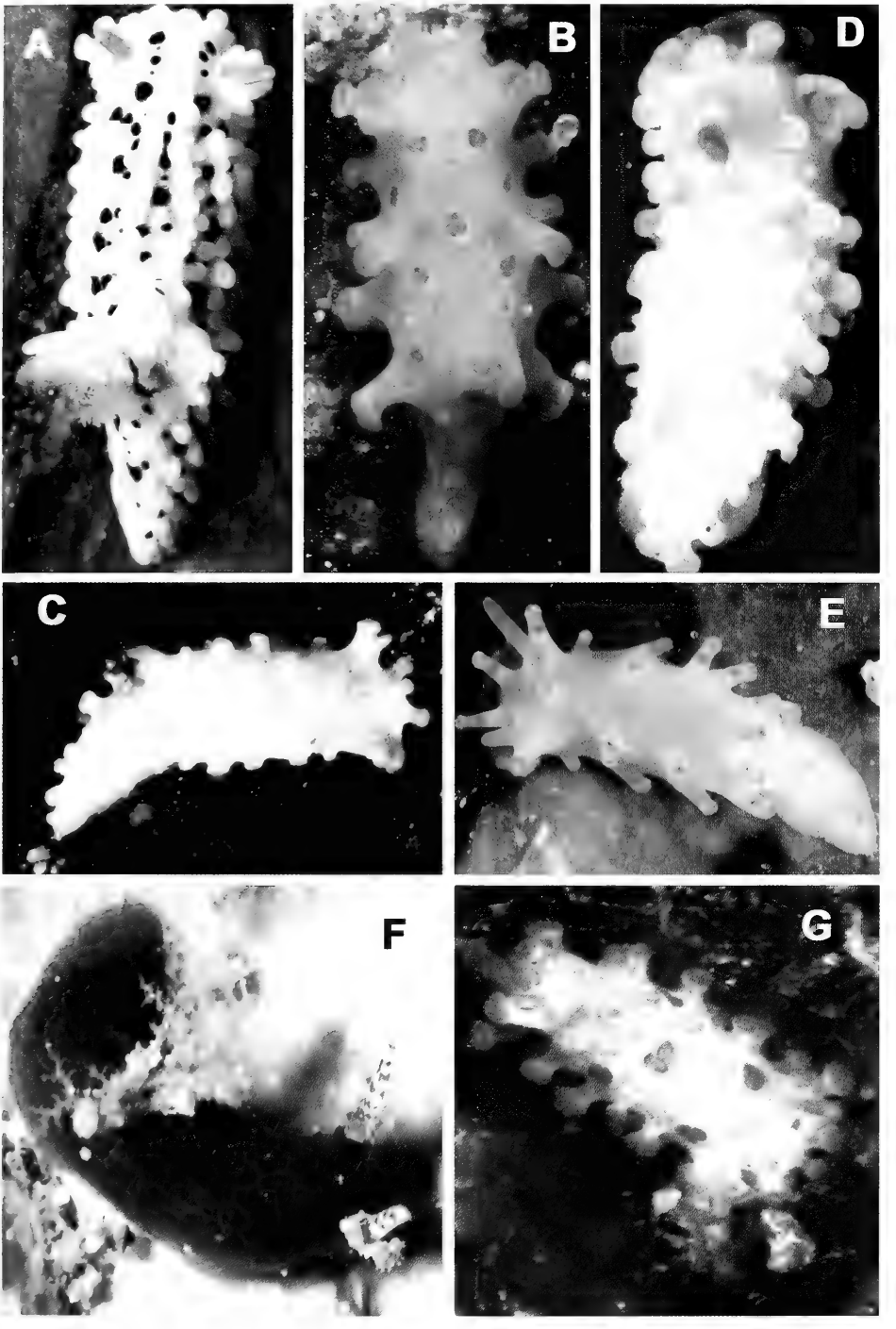
(Figs. 1A, 2–6)

Aegires albopunctatus MacFarland, 1905:35-54, pl. 18, Figs 5-8.

Type material.— Syntype: Monterey Bay, California, No. 181,281. U.S. National Museum.

Material examined.— LACM 127330, one specimen, 18 mm, dissected, Rio San Ysidro, Baja California, collected 28 June 1946, C. Johnson. LACM 71-36, one specimen, 18 mm, dissected, Point Dume, Southern California, collected 8 February 1971, G. Sphon. LACM 90-2.3, one specimen, 7 mm, dissected, Cabo Colnett, Baja California, collected 10 February 1990, collector not specified. CASIZ 118550, one specimen, 20 mm, dissected, Pacific Coast, Baja California North, collected 3 February 1963, W. Farmer. CASIZ 068347, nineteen specimens, one specimen, 20 mm dissected, Corona del Mar, Southern California, collected 4 May 1946, F. MacFarland. CASIZ 068349, five specimens, one specimen, 20 mm, dissected, Cannery Row, Monterey Bay, California, collected 28 September 1968, A. Smith.

Figure 1. Living animals. (A) *Aegires albopunctatus* MacFarland, 1905. CASIZ 118550, photo by A. Ferreira, Monterey Bay, California, 19 mm. (B) *Aegires pruvotfolae* nom. nov. CASIZ 097449, photo by T. Gosliner, Napili Bay, Maui, Hawaii, 6 mm. (C) *Aegires gomezi* Ortea, Luque and Templado, 1990. CASIZ 077315, photo by T. Gosliner, Grand Cayman Island, 5 mm. (D) *Aegires ninguis*.sp. nov. CASIZ 073982, photo by T. Gosliner, Cape Province, South Africa, 8 mm. (E) *Aegires lemoncello* sp. nov. CASIZ 086465, photo by T. Gosliner, Pig Island, Papua New Guinea, 4 mm. (F) *Aegires malinus* sp. nov. CASIZ 085889, photo by T. Gosliner, Bebbit, Philippines, 8 mm. (G) *Aegires incusus* sp. nov. CASIZ 156668, photo by T. Gosliner, Cemetary Beach, Luzon, Philippines, 5 mm.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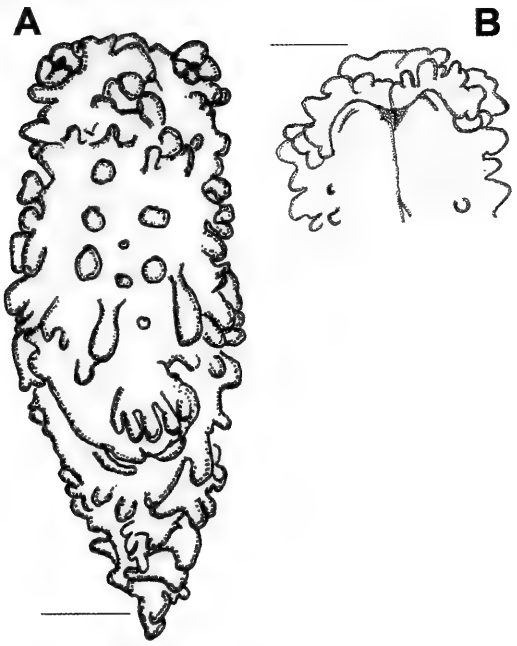


FIGURE 2. *Aegires albopunctatus* MacFarland, 1905. CASIZ 118550. Drawing of preserved specimen. (A) Dorsal view. (B) Ventral view of head. Scale = 7 mm.

DISTRIBUTION.— West coast of North America from British Columbia to Baja California ([Behrens 1991] Rudman, SeaSlug Forum, accessed Sept. 2004).

EXTERNAL MORPHOLOGY.— MacFarland (1905, 1906, 1966) gave thorough descriptions of the external morphology of this species. The specimens examined for the present study matched his descriptions and thus there is no additional information to present. See Fig. 1A for a photo of a living animal from the type locality and Fig. 2 for a drawing of a preserved specimen from Baja California.

DIGESTIVE SYSTEM.— *Aegires albopunctatus* shares the same general digestive anatomy as other *Aegires* species (Fig. 3). The buccal bulb is nearly round, with four large muscles attached; two per side. The buccal bulb is shorter and more round than the oral tube (Fig. 3A). There are two glands at the side of the oral tube, near the mouth (Fig. 3B). The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is

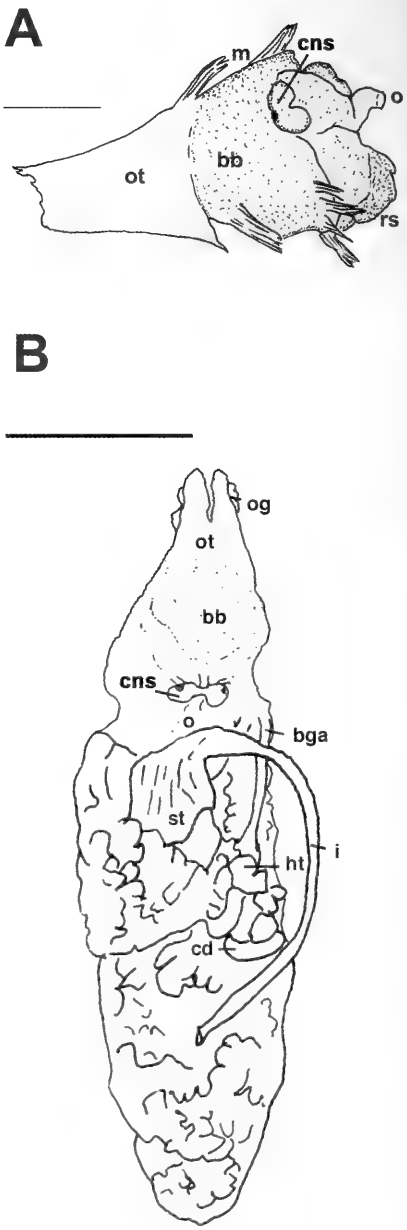


FIGURE 3. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. (A) Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, o = esophagus, rs = radular sac, scale = 0.3 mm. (B) Digestive system: bb = buccal bulb, bga = blood gland artery, cd = collecting ducts, cns = central nervous system, ht = heart, i = intestine, o = esophagus, og = oral gland, ot = oral tube, st = stomach, scale = 3 mm.

lined with a thick cuticle. There is a thick plate at the top of the opening, with thick rods at the edge (Fig. 4A). The radular formula (CASIZ 118550) is $19 \times 21.0.21$, with all teeth as described by MacFarland. That is, they are simple, hooked and similar in form (Figs. 4B–D). The esophagus is short and connects directly to the stomach (Fig. 6). The intestine makes a simple, wide curve along the outside of the digestive gland.

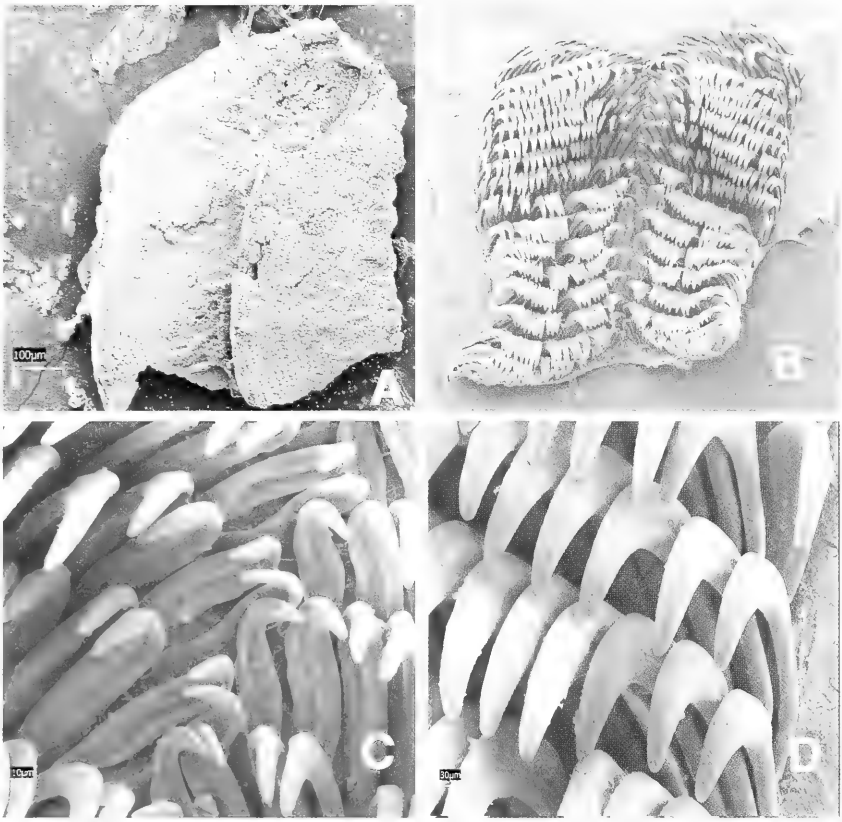


FIGURE 4. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. Buccal morphology. (A) Jaw, scale =100 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 30 µm.

REPRODUCTIVE SYSTEM.— The ampulla is large and ovoid (Fig. 5). It branches into the oviduct and the tubular prostate. The hermaphroditic duct enters the ampulla terminally. The thin oviduct enters the large female gland mass. The prostate is differentiated into two parts, the proximal portion being a flattened mass and the distal portion being a long thickened tube. The distal portion folds once after exiting the flattened mass and narrows into the coiled deferent duct. The penis is wider than the deferent duct and terminates into a common genital atrium. The penis contains minute, closely set penial hooks throughout the length of the penis. The vaginal duct is short and wide. It was not examined internally and thus the presence of spines or hooks cannot be confirmed.

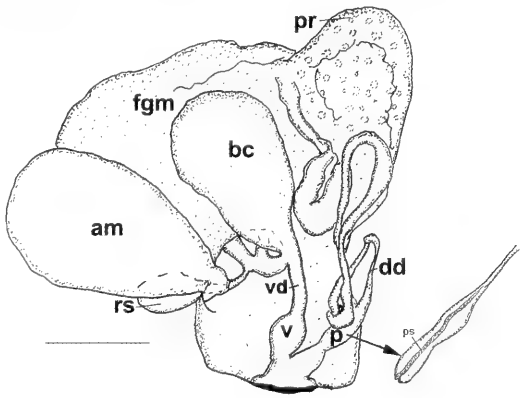


FIGURE 5. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 1 mm.

At the distal end, the vagina is wide and bulbous. The proximal end terminates into the large ovoid bursa copulatrix. From the bursa the oviduct connects to the smaller pyriform receptaculum seminis. A very short uterine duct leads from the receptaculum seminis into the female gland mass.

Central nervous system.— As with other species of *Aegires*, the cerebral and pleural ganglia are fused together (Fig. 6). The two pedal ganglia are located below the cerebro-pleural complex and are joined by an elongate commissure. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. The eyes are sessile at the cerebro-pleural juncture. There are four cerebral nerves leading from each cerebral ganglion including the rhinophoral ganglia, and two large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

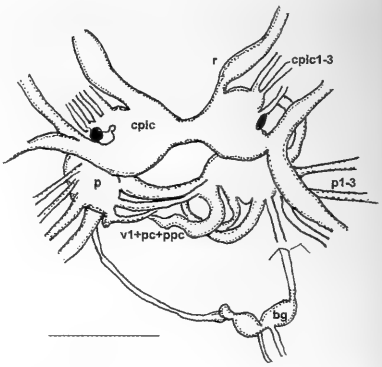


Figure 6. *Aegires albopunctatus* MacFarland, 1905. LACM 127330. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.3 mm.

Remarks.— MacFarland (1905, 1906, 1966) presented thorough external and radular descriptions of this northeastern Pacific species. Anatomical information for the present study has been taken from his paper and corroborated by examining specimens from the type locality and the southern California coast. Ernst Marcus (1961) also published additional anatomical details of this species. However, some characters that were necessary for the present study such as the circulatory, central nervous or digestive systems were not described. Therefore, additional specimens were examined to complete the data.

Risbec (1928) synonymized *A. albopunctatus* MacFarland, 1905 with *A. leuckartii* Verany, 1853 in his lengthy description of *A. leuckartii*. Marcus (1961) noted some external similarity between *A. albopunctatus* and *A. punctilucens* stating that *A. albopunctatus* "agrees with the type species *A. punctilucens*" based upon the papillae on the mantle border of both species.

No other subsequent publications referring to *A. punctilucens* or *A. leuckartii* recognized the synonymy of either species with *A. albopunctatus* (Pruvot-Fol 1954; Fischer et al. 1968; Nordsieck 1972; Schmekel and Portmann 1982; Thompson and Brown 1984). However, Haefelfinger (1968) did synonymize *A. leuckartii* with *A. punctilucens* based upon characters that he thought lie within natural variation. But subsequently, Schmekel and Portmann (1982) separated *A. punctilucens* and *A. leuckartii* as subspecies, distinguishable by their ecology and reproductive cycles. Further remarks on this synonymy are presented under the sections discussing these two species.

The present study confirms that *Aegires albopunctatus* is a valid species with the following characters distinguishing it from *Aegires punctilucens*:

1. External color. *Aegires punctilucens* has very distinctly colored spots on the dorsum. These spots have been described by various authors (Thompson and Brown 1984) as resembling an ocellus: that is, dark brown oval areas containing an iridescent blue-green spot, with or without additional dark spots on the periphery of the ocellated markings. In contrast, MacFarland's description of *A. albopunctatus* is very clear in that the dorsum only has minute dots of pure white, with or without irregularly scattered small dark brown spots. No ocellus spots are noted on any of his specimens.

2. Dorsal tubercle arrangement. *Aegires albopunctatus* has very densely placed tubercles, closely set in rows and continuing behind the rhinophores as a tuberculate ridge that diminishes in prominence

(MacFarland 1905). *Aegires punctilucens* has more widely scattered, larger tubercles that continue as a tuberculate ridge in a crest along the middle of the back (Schmekel and Portmann 1982).

3. Reproductive characters. *Aegires albopunctatus* has two ducts emerging from the base of the bursa copulatrix, while *A. punctilucens* has only one. The receptaculum seminis duct emerges from the proximal end of the large, bulbous vagina. Additionally, the vagina of *A. albopunctatus* is much more elongate than that of *A. punctilucens*.

4. Radular formula. Schmekel and Portmann (1982) reported a radular formula of 16 × 18.0.18 for a 6 mm specimen of *A. punctilucens* with the size of the teeth increasing outwards. Thompson's (1984) 12 mm specimen of *A. punctilucens* from the Isle of Man had a radular formula of 23 × 22.0.22 with the teeth from the midline having a hooked tip, but the teeth from the margins were reported as more smoothly hooked. These reports on the radular formulae differ from MacFarland's reported formula for a 13 mm specimen of *A. albopunctatus* of 16–22 × 17.0.17 with the innermost and outermost teeth being similar in size but smaller than the middle lateral teeth. (See also Fig. 4).

Aegires albus Thiele, 1912

Aegires albus Thiele, 1912:222.
Anaegires protectus Odhner, 1934:242.
Aegires protectus (Odhner) Wägele, 1987:271.

Type material.— Holotype: No. 63230 (*A. albus*), McMurdo Sound, Antarctica. Zoologisches Museum zu Berlin; Other material: No. 846 (*A. albus*) Naturhistoriska Riksmuseet, Stockholm; Holotype: No. 1934.10.5.67 (*A. protectus*), British Museum of Natural History, London.

Material examined.— *Aegires albus* from the Muséum National d'Histoire Naturelle, Paris: Kerguelen Islands, 1 specimen, collected at 15 m, 16 January 1963, no further collection data provided; MD04 G65 DC 155, 1 specimen, no further collection data provided; SMK, 10 specimens, 15–144 m, collected 1972 and 1974 by Guille et al.

Distribution.— This species has only been recorded from the Antarctic Peninsula, the Ross Sea and the Weddell Sea (Wägele 1987).

Remarks.— *Aegires protectus* is the type species of *Anaegires* Odhner, 1934. *Anaegires* is a synonym of *Aegires* (see Odhner 1934). Wägele (1987) presented a thorough description of *Aegires albus,* with both external and internal anatomy. She demonstrated that *Aegires protectus* is a synonym of this species. Anatomical information has been taken from this publication and from the specimens noted above for use in the present study. Examination of the reproductive system of specimens listed above confirmed the presence of densely placed penial spines extending the length of the penial bulb as reported by Wägele (1987).

Aegires pruvotfolae Fahey and Gosliner, nom. nov.

(Figs. 1B, 7–11)

Aegires citrinus Pruvot-Fol, 1930:229-232, junior homonym of *Aegires citrinus* (Bergh, 1875). (See the discussion of *Aegires citrinus*).

Type material.— Collected in New Caledonia, date and collector not specified. Neotype here designated, CASIZ 157477, one specimen, 6 mm, Layag Layag, Caban Island, Philippines, collected T. Gosliner.

Material examined.— CASIZ 097449, one specimen, 6 mm, dissected, Napili Point, Maui, Hawaii, no depth available, collected 9 April 1994, T. Gosliner. CASIZ 087056, one specimen, 10 mm, Keahou Beach, Hawaii, no depth available, collected 3 September 1973, T. Gosliner. CASIZ

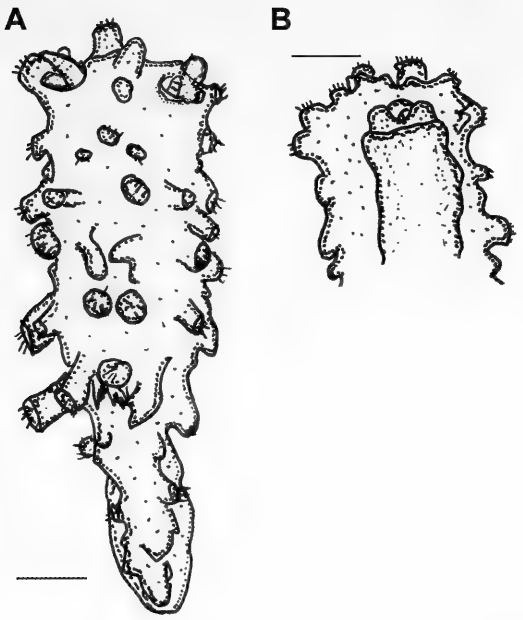


FIGURE 7. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Drawing of preserved specimen. (A) Dorsal view. (B) Ventral view of head. Scale = 0.4 mm.

087058, three specimens, no depth available, collected 19 February 1986, T. Gosliner. CASIZ 070326, one specimen, 3 mm, dissected, Nosy Tanikely, Madagascar, 1 m depth, collected 14 April 1989, T. Gosliner. CASIZ 088363, one specimen, 8 mm, dissected, Midway Island, Pacific Ocean, 10 m, collected 29 May 1993, T. Gosliner. CASIZ 099286, one specimen, 6 mm, Manahuanja Island, Tanzania, collected 1 Nov 1994, T. Gosliner.

DISTRIBUTION.— This species has been recorded from eastern Australia, New Caledonia, the Philippines, Hawaii, Palau, Midway Atoll, Tanzania and Madagascar (Rudman 2004 and present study).

EXTERNAL MORPHOLOGY.— The body shape is high and arched (Figs. 1B, 7). The dorsum has tall, anvil-shaped tubercles with flat tops. Spicules protrude from the tops of all tubercles. The rhinophore pocket is elevated and has one tall tubercle on the outside perimeter. There are two prominent tubercles on the head. The posterior end of the foot has low

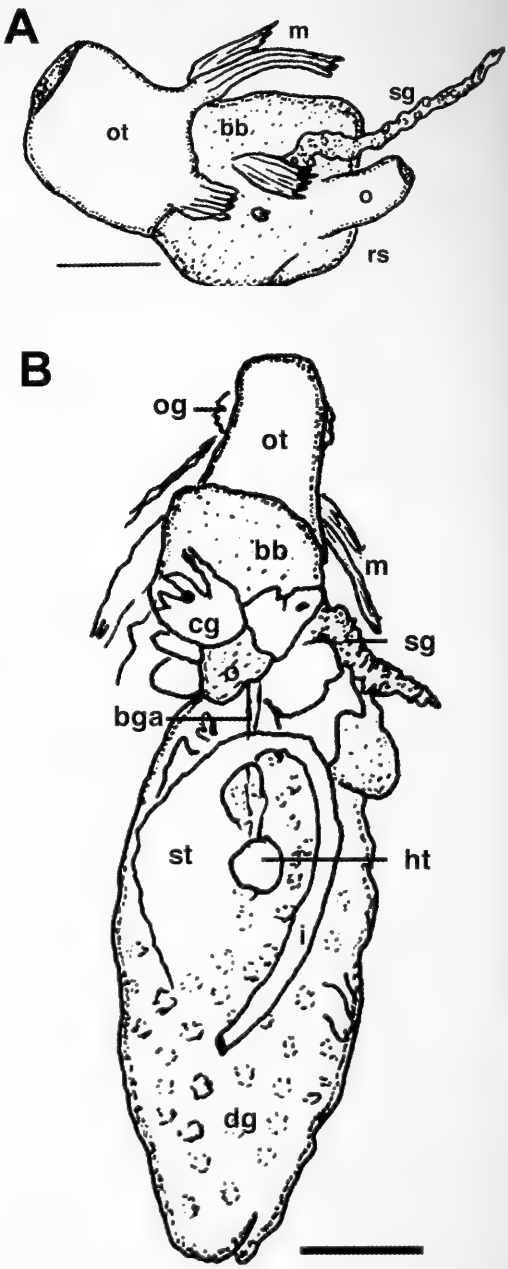


FIGURE 8. *Aegires pruvotfolae* nom. nov. CASIZ 097449. (A) Buccal bulb: bb = buccal bulb, m = muscle, o = esophagus, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.25 mm. (B) Digestive system: bb = buccal bulb, bga = blood gland artery, cg = cerebral ganglia, cns = central nervous system; ht = heart, i = intestine, m = muscle, og = oral gland, ot = oral tube, sg = salivary gland, st = stomach, scale = 0.25 mm.

tubercles that are much smaller than those on the dorsum. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and three large anvil-shaped tubercles protect the anterior side of the gill pocket. The three small gill leaves are tripinnate.

The background color is pale to medium yellow. The tubercles are the same color, as are the rhinophores. There are light brown to tan spots that vary in size along the dorsum median, between the tubercles.

Digestive system.— *Aegires pruvotfolae* shares the same general digestive anatomy as other *Aegires* species. That is, there are two glands at the side of the oral tube, near the mouth (Fig. 8). The buccal bulb is nearly round, with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with thick rods at the edge (Fig. 9A). The radular formula is 16 × 11.0.11. The teeth are simply hamate and the three innermost lateral teeth are smaller than the remaining teeth (Figs. 9B–D). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

Reproductive system.— The ampulla is relatively small and compact. It branches into a short oviduct and the prostate (Fig. 10). The oviduct enters the female gland mass near its center.

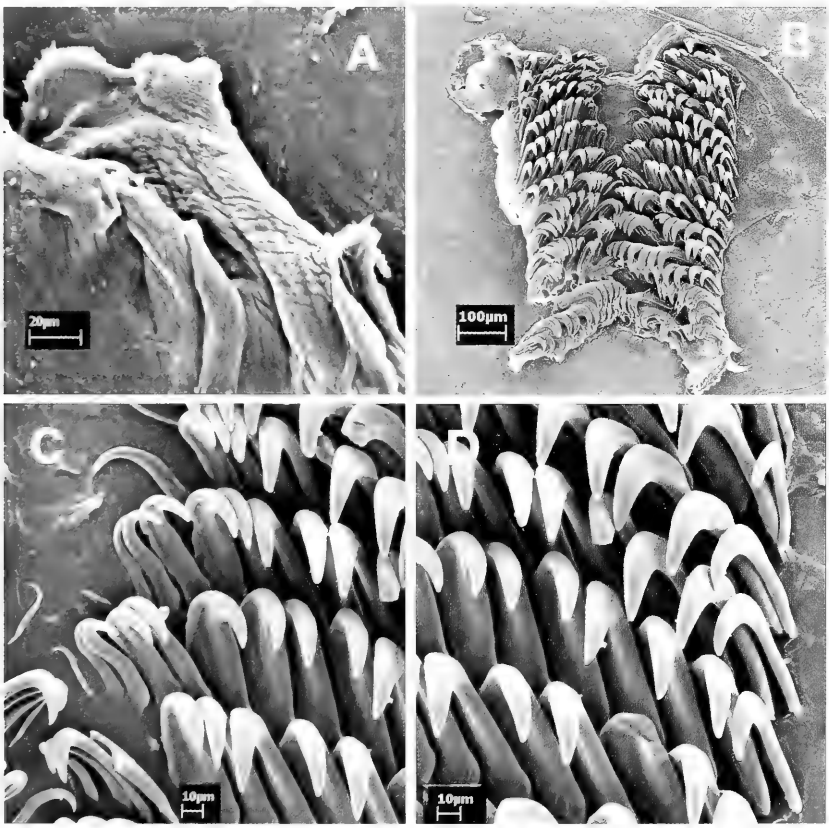


FIGURE 9. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Buccal morphology: (A) Jaw, scale = 20 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm.

The prostate is very long, tubular and coiled. It narrows slightly then connects to a wide ejaculatory duct and terminates at the wide penis. There are densely spaced, small hooks inside the penis at the distal tip only. The vagina is short and wide. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At its proximal end the vaginal duct joins the bursa copulatrix and the seminal receptacle. The uterine duct also leads from this duct. The bursa is spherical and the receptaculum seminis is about the same size though elongated.

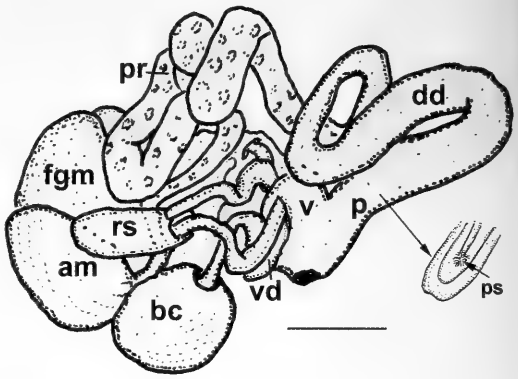


FIGURE 10. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.2 mm.

CIRCULATORY SYSTEM.— The heart (Fig. 8) is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

CENTRAL NERVOUS SYSTEM.— As with other species of *Aegires*, the cerebral and pleural ganglia are fused together (Fig. 11). The two pedal ganglia are located below the cerebro-pleural complex and are joined by pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are placed under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively short nerves. There are four cerebral nerves leading from each cerebral ganglion, and three pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

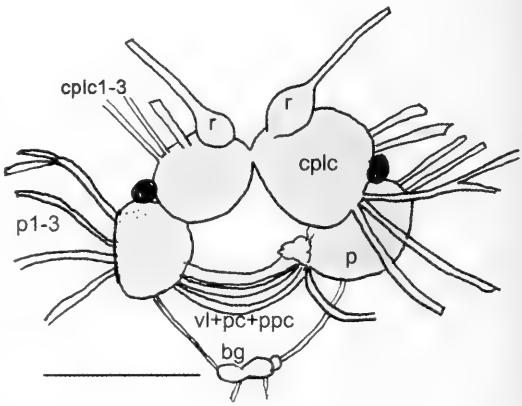


FIGURE 11. *Aegires pruvotfolae* nom. nov. CASIZ 097449. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.2 mm.

REMARKS.— Pruvot-Fol (1930) presented a very abbreviated description of *Aegires citrinus* collected from New Caledonia. The only information she provided on this new species was that the color was lemon yellow and the specimen had pointed tubercles with light brown color at the tops. Pruvot-Fol wrote that *A. citrinus* resembled *Aegires leuckartii* Verany, 1853 and may be a variant of the latter. We discuss this species in the comparison section below.

Risbec (1953) briefly mentioned Pruvot-Fol's abbreviated description of *A. citrinus*. He thought that since no precise detailed description had been published, *A. citrinus* was probably a variation of *A. leuckartii* (see discussion below).

Rudman (2004) provided additional external morphological information from photographs taken of this species.

For the present study, specimens from the Indian Ocean, Hawaii and Midway Island, Pacific Ocean were examined. This study has revealed that *A. pruvotfolae* is a valid species having sever-

al characteristics that differ from the other *Aegires* species. Those characters are:

1. External coloration. *Aegires pruvotfolae* is similar in coloration to *A. incusus* (present study). That is, both species can have a pale yellow background color and light brown to tan dorsal spots. However, the tubercle color of *A pruvotfolae* is also yellow with tan apices, whereas *A. incusus* has brown to tan tubercles with a darker top. The rhinophores of *A. pruvotfolae* have a tan top whereas those of *A. incusus* do not.
2. Tubercle spicules. The spicules that project from the tops of the tubercles of *A. pruvotfolae* are low and less conspicuous than those of *A. incusus*.
3. Tubercle arrangement. There are two prominent flat-topped tubercles on the head of specimens of *A pruvotfolae*. On *A. incusus*, there are multiple tubercles on the head. The dorsal tubercles of *A pruvotfolae* are less numerous than on specimens of *A. incusus*.
4. Radular characters. *Aegires pruvotfolae* has one small, thin inner lateral tooth that has a very small hook; the next 3–4 inner lateral teeth are smaller than the remainder. All other lateral teeth are the same size. In *A. incusus*, there is also one small inner lateral tooth but it has a distinct hook. The next 2–3 teeth are smaller than the remaining teeth, which are all the same size. In addition, the radular sac does not protrude from the buccal bulb in *A. citrinus* as it does in *A. incusus*.
5. Reproductive characters. *Aegires pruvotfolae* has reproductive characters that distinguish it from the most similar *Aegires* species. Most noticeably, the vagina is very wide as compared to *A. incusus*. In addition, the bursa copulatrix of *A. pruvotfolae* is as large as the ampulla, whereas in *A. incusus* the bursa is comparatively much smaller. The prostate of *A. pruvotfolae* is very long and coiled and does not narrow appreciably before entering the deferent duct. In *A. incusus* the prostate is not nearly as long and it does narrow noticeably before entering the deferent duct.

Aegires pruvotfolae also bears some external resemblance to early descriptions of *A. leuckartii*. For example, Schmekel and Portmann (1982) reported both white and brown specimens of *A. leuckartii*. They found that the brown specimens had "somewhat symmetrically arranged, smooth, brown areas, which were not circular". These spots are similar to those found on *A. pruvotfolae*. Risbec (1953) also considered *Aegires pruvotfolae* (formerly *Aegires citrinus*) a probable variation of *A. leuckartii*. However, there are external and internal differences that separate these two species:

1. The foot, veil and oral tentacles of *A. leuckartii* are bluish-white while in *A. pruvotfolae* the entire body, both dorsal and ventral surfaces are pale to muddy yellow. *Aegires pruvotfolae* has yellow rhinophores while the rhinophores of *A. leuckartii* have brown tips and 3 white circles (see Vérany 1853).
2. The dorsal tubercle arrangement differs between these two species. *Aegires leuckartii* has 4 large tubercles on the rhinophore sheath, whereas on *A. pruvotfolae* there are only 3.
3. The dorsal tubercle shape also differs between these two. *Aegires leuckartii* has cylindrical or rounded tubercles while the tubercles of *A. pruvotfolae* are anvil or mushroom-shaped.
4. There is also a difference in the radular morphology between these two species. Schmekel and Portmann reported that the teeth of *A. leuckartii* are all of similar size, whereas in *A. pruvotfolae* the innermost radular tooth is the smallest, then there are 3–4 small teeth and the remainder are all the same size.
5. Vérany did not describe the reproductive morphology of *A. leuckartii* but Schmekel and Portmann (1982) considered that the reproductive anatomy of *A. leukartii* was essentially as found with *A. punctilucens*. As such, there are differences between the reproductive morphology of *A. punctilucens* and *A. pruvotfolae*. We describe the morphology of *A. pruvotfolae* in an earlier section. But to summarize the differences, the prostate in *A. punctilucens* is rounded and in two parts. In *A. pruvotfolae* the prostate is very long, tubular and coiled. The vaginal duct in *A. punctilucens* is very short whereas in *A. pruvotfolae* it is very long. The receptaculum seminis of *A. punctilucens* connects to the uterine duct on a short duct. But in *A. pruvotfolae* this duct is very long and coiled.

The differences in external and internal morphology between *A. leuckartii*, *A. punctilucens, A. pruvotfolae* and *A. incusus* distinguish these four as separate *Aegires* species.

Aegires gomezi Ortea, Luque, and Templado, 1990

(Figs. 1C, 12C–D, 13–15)

Aegires gomezi Ortea, Luque, and Templado, 1990:333, Figs 1–2.

Type material.— Holotype: 15.05/1034, La Habana, Cuba, Museo Nacional de Ciencias Naturales of Madrid.

Material examined.— Holotype: MNCN 15.05/1034, one specimen, 2 mm, La Habana, Cuba, collected July 1988, D. Moreno. CASIZ 077320, one specimen, 5 mm, dissected. Grand Cayman Island, no depth available, collected May 1991, T. Gosliner. CASIZ 077315, one specimen, 3 mm, South Sound, Cayman Islands, no depth available, collected May 1991, T. Gosliner. LACM 2003-41.1, one specimen, 5 mm, dissected. Key Largo, Florida, collected July 2003, A. Valdés.

Distribution.— This species was reported from La Habana, Cuba in the original description (Ortea, Luque, and Templado 1990) and from Florida and the Cayman Islands (this study).

External morphology.— The external morphology of the specimens collected in the Cayman Islands matches that of the original (1987) description of *A. gomezi*. The color photo of the Cayman specimens (Fig. 1C) matches the descriptions by Templado et al. (1987) and Ortea et al. (1990)

Digestive system.— The digestive system of the 5 mm specimen collected in Cayman Islands in 1991 was examined for the present study. The buccal bulb is nearly round, with the radular sac protruding noticeably from the posterior end. There are two long salivary glands extending from under the esophagus. As found in other species of *Aegires*, there are four main muscles attached at the midpoint of the buccal bulb (Fig. 13). The radular formula of this specimen is 18 × 12.0.12 (Fig. 14). The teeth are simply hamate as reported for the holotype. The jaw has numerous rodlets (Fig. 14D).

Reproductive system.— One of the specimens from the Cayman Islands was dissected for the present study. The reproductive system is triaulic. The ampulla is elongate. It branches into a short oviduct and the prostate (Fig. 15). The oviduct enters the female gland mass near an edge.

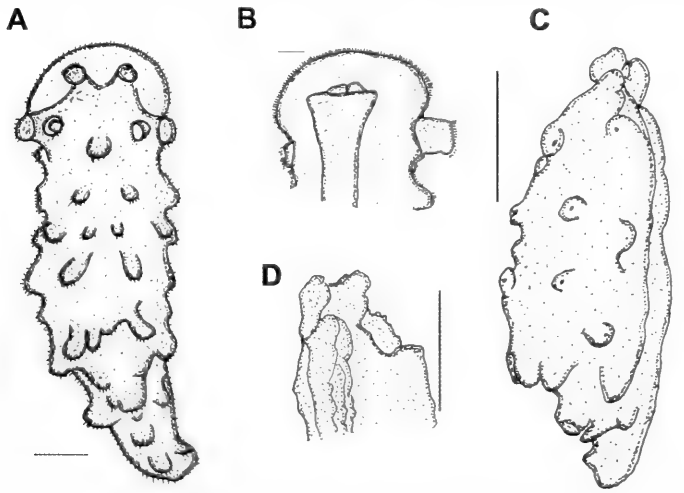


Figure 12. Drawings of preserved animals. *Aegires ortizi* Templado, Luque, and Ortea, 1987. MNCN12-64/1006. (A) Dorsal view. (B) Ventral view of head. Scale = 0.7 mm. (C) *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Dorsal view. (D) Ventral view of head. Scale = 0.7 mm.

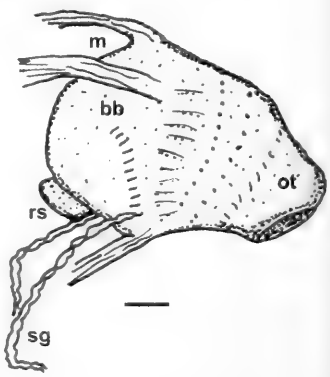


Figure 13. *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Buccal bulb: bb = buccal bulb, m = muscle, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.13 mm.

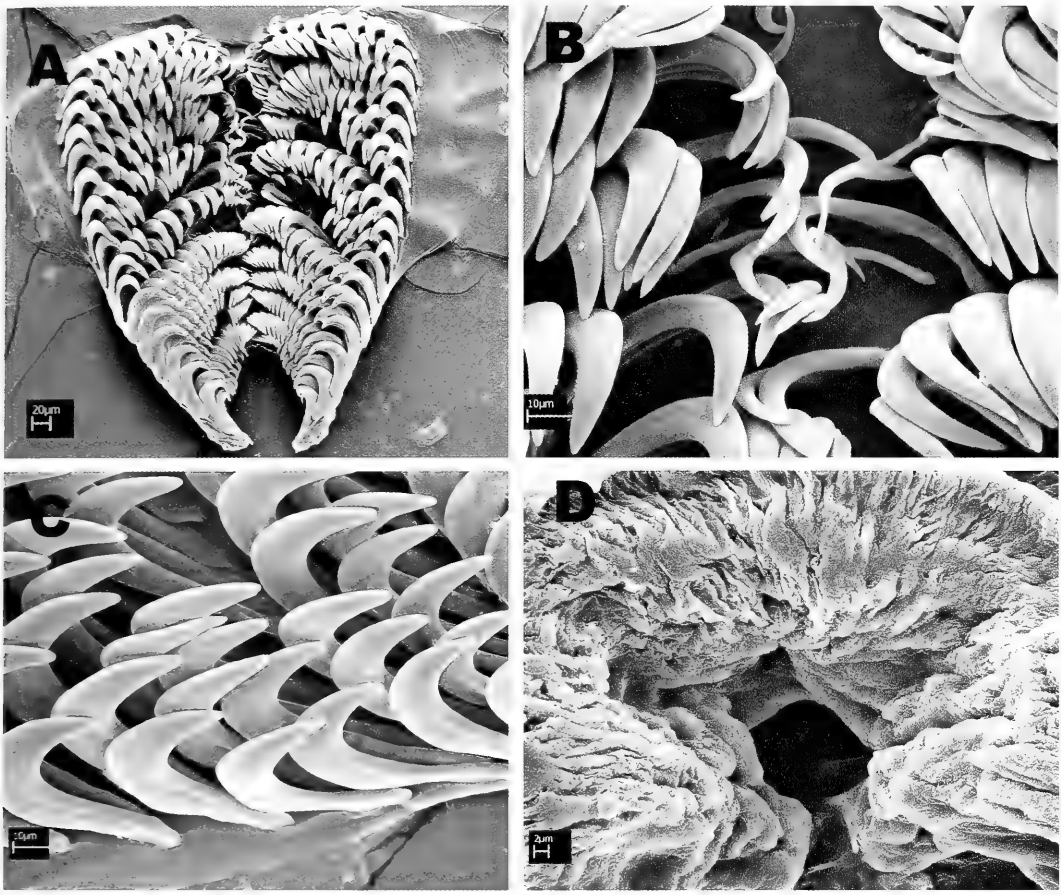
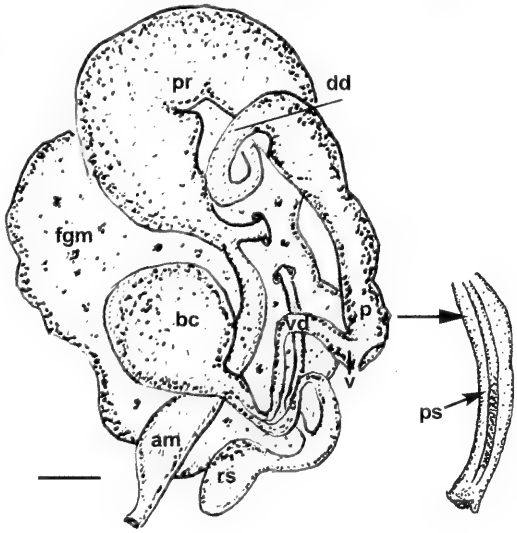


FIGURE 14. *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Buccal morphology: (A) Whole radula, scale = 20 µm. (B) Inner lateral teeth, scale = 10 µm. (C) Outer lateral teeth, scale = 10 µm. (D) Jaw, scale = 2 µm.

FIGURE 15. *Aegires gomezi* Ortea, Luque, and Templado, 1990. CASIZ 077320. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.08 mm.



The prostate is a thick, coiled tube. It narrows into a small, coiled tube, then connects to a very wide ejaculatory duct and terminates at the glans penis. There are densely packed, small hooks inside the penis extending the entire length of the penial bulb. The vagina is long and narrow. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At its proximal end it joins the bursa copulatrix. A long separate duct joins the receptaculum seminis to the base of the bursa, and also connects to the female gland mass near the same edge as the oviduct. The bursa is large, spherical and the receptaculum seminis is about one-third the size of the bursa.

Central nervous system.— The central nervous system was not available for examination.

Remarks.— Ortea et al. (1990) described this species from a single specimen collected in 1988 from a tidepool in La Habana, Cuba. Their description included the external and radular morphology, but the reproductive, central nervous system and digestive systems were not described.

Aegires leuckartii Verany, 1853

Aegires leuckartii Verany, 1853:388.
Aegires leuckartii (Verany) Bergh, 1883:135.
Aegires leuckarti (Verany) Vayssière 1901:55ff.
Aegires leuckarti (Verany) Risbec, 1953: 60.
Aegires leuckarti (Verany) Pruvot-Fol, 1954:245.
Aegires leuckarti (Verany) Haefelfinger, 1960c:355.
Aegires leuckarti (Verany) Schmekel, 1968b:116.
Aegires punctilucens leuckarti, Schmekel and Portmann, 1982:102.

Type material.— Verany described this species from a single specimen collected from Nice, France. Attempts to locate the type specimen were unsuccessful.

External morphology.— In the original description, the external morphology and coloration of *Aegires leuckartii* was the only information provided by Verany of the specimen collected. To summarize: The body shape of this species is wedge-shaped, with a straight or flat anterior and terminating in a pointed tail. There is no mantle edge and there is a large frontal veil with rounded lateral lobes. The rhinophore pocket is shaped like a large "horn" that is irregularly trilobed. The three gill leaves are very small, bipinnate and at the anterior and lateral edge of the gill pocket are large tubercles. These are conical and concave, larger along the median and smaller along the edge and scattered fairly regularly on the dorsum. The foot, the frontal veil, the oral tentacles are all bluish-white and the dorsum is yellowish-brown, light along the edges and darker in the center. There are brown spots on the dorsum. The tips of the rhinophores are brown with three white circles.

Verany chose the particular spelling of *leuckartii* for this new species. Subsequent authors, beginning with Vayssière (1901) dropped the last '*i*'. However, the *International Code of Zoological Nomenclature* allows for the Latinate spelling designated by the original author, thus *leuckartii* is correct.

As mentioned previously, Pruvot-Fol (1930) described a specimen of *A. pruvotfolae* from New Caledonia. Risbec thought her specimen was *A. leuckartii*, similar to a specimen he found in New Caledonia. Both these specimens are most likely *A. pruvotfolae*. See the comparison of these species under *A. pruvotfolae*.

Distribution.— This species is only found in the Mediterranean.

Remarks.— Schmekel and Portmann (1982) described *Aegires punctilucens leuckartii* from Nice, France. They reported external differences from Risbec's New Caledonian specimens that he collected and identified as *A. punctilucens*. (But, see the discussion under *A. pruvotfolae.*) The dor-

sal tubercles on the specimens from France were reported to be cylindrical and/or rounded, as described by MacFarland for *A. albopunctatus*, and not flat tubercles as reported by Risbec. Additionally, Schmekel and Portmann reported three tubercles arranged in a line in the mid-dorsal region, with three large tubercles on the outer edge of the rhinophore sheaths, and several smaller ones on the inner side. Risbec noted four large papillae on the rhinophore sheath.

There are some differences in external coloration between Schmekel and Portmann's specimens and Risbec's. Risbec does not mention the opaque white dots scattered on the dorsum that Schmekel and Portmann observed and also noted by MacFarland for *A. albopunctatus*. Both Risbec and Schmekel and Portmann report dark spots on the foot but MacFarland observed only white on the foot. The color of the rhinophores differs in that the specimens from France had a transverse brown ring, and the tips of the gill leaves were opaque white. Risbec reported only grayish rhinophores and translucent gill leaves and MacFarland reported lemon yellow rhinophores and gill leaves with spots.

The observations of the radular teeth of specimens from the Mediterranean indicate that all teeth were of similar size. The radular formula reported for a 6 mm specimen was 16 × 15.0.15 (Schmekel and Portmann 1982). Bergh (1883) reported a radular formula of 17 × 15–16.0.15–16 for an 8 mm specimen from Trieste.

Schmekel and Portmann's description of *Aegires punctilucens leuckartii* most nearly matches that of *A. albopunctatus* MacFarland, whereas Risbec's description of specimens collected from New Caledonia most nearly match that of *A. leuckartii* Verany.

Nordsieck (1972) listed *A. leuckartii* as a synonym of *A. punctilucens*, but without any justification. The specimens he described externally match *A. punctilucens*.

Regarding the status of *Aegires leuckartii*: without having the description of the reproductive morphology from original material, it would be confusing to synonymize this species with *A. punctilucens* (see Haefelfinger 1968). Descriptions of the background color of *A. leuckartii* are most similar to *A. albopunctatus*, not *A. punctilucens*. The body shape and tubercle arrangement of *A. punctilucens* as illustrated by d'Orbigny (1837) does not match the original description of *A. leuckartii* Verany. The radular formula of *A. leuckartii* noted by Risbec (1928) was 16 × 12.0.12 for a 6 mm specimen and Schmekel and Portmann (1982) reported the formula for an 8 mm specimen of *A. punctilucens leuckartii* as 16 × 15.0.15. Schmekel and Portmann also reported that the teeth increase in size outwards, as they found in *A. punctilucens*.

Schmekel and Portmann also noted the difference in the gill structure between *A. leuckartii* and *A. punctilucens*. The former has bipinnate gill leaves while the latter has a tripinnate structure. MacFarland described *A. albopunctatus* as having three small tripinnate gill leaves.

Schmekel and Portmann did not agree with Haefelfinger's synonymy and stated that the morphological and ecological differences they observed clearly distinguish *A. punctilucens* from *A. leuckartii*. On the same basis, examination of *A. albopunctatus* indicates that it too, should be considered distinct from these two as noted in the previous discussion of *A. albopunctatus* (present study).

Photo images of specimens collected from the Mediterranean and identified as *A. leuckartii* and *A.* cf. *leuckartii* are most likely *A. leuckartii* (Koehler 2004; Tocino 2004).

Aegires palensis Ortea, Luque and Templado, 1990 is a probable synonym of *A. leuckartii.* Ortea, Luque, and Templado did not compare their specimen to *A. leuckartii* because they considered *A. leuckartii* as a synonym of *A. punctilucens*.

Risbec (1928, 1953) synonymized *A. leuckartii* with *A. albopunctatus*, in lengthy descriptions of specimens he collected from New Caledonia as discussed above. His specimens are most likely *A. pruvotfolae* as discussed below and in the Remarks section of *A. pruvotfolae*.

Externally, Risbec described his specimens as thin, wedge-shaped and elongate with a pointed posterior end of the foot. *Aegires albopunctatus* in contrast has a high, rounded dorsum with a rounded tail (MacFarland 1966). The dorsal tubercles described and illustrated by Risbec are all flattened and less numerous than those illustrated by MacFarland who reported both rounded and flattened tubercles. Risbec illustrates a specimen with three distinct rows of dorsal tubercles, whereas MacFarland describes tubercles that are more numerous and larger toward the end of the dorsum behind the gill. MacFarland describes the tubercles as forming three rows, only behind the gill. Also, the large gill-protective tubercles on Risbec's specimens are shown as much smaller and more simple than those illustrated by MacFarland.

The external coloration also differs between Risbec's specimens and *Aegires albopunctatus*. Risbec's have grayish rhinophores and the rhinophores on *A. albopunctatus* are lemon yellow with tiny dots of white (MacFarland 1966). The gill plumes of Risbec's specimens are pale yellow with tiny opaque white dots, while those of MacFarland have no dark pigment except for occasional spots (color unspecified by MacFarland). Risbec reports a faint greenish border on the foot, whereas MacFarland mentions white as the only color on the foot of *A. albopunctatus*.

There are radular differences as well. The teeth of Risbec's specimens (1928) have a straighter hook than does *A. albopunctatus*. Risbec reported that all radular teeth of his specimens were of similar size. But MacFarland noted that the teeth of *A. albopunctatus* gradually increased in size from the center, with the outermost tooth being smaller than the rest. The radular formula reported for Risbec's specimen is 16 × 12.0.12 for a 6 mm specimen, whereas MacFarland reports a formula of 16-22 × 17.0.17 for *A. albopunctatus* specimens averaging 13 mm.

Although both authors provided a very limited description of the reproductive system, they both noted that the penis is armed with many small hooks.

It seems likely that the specimens described by Risbec were not *Aegires albopunctatus* MacFarland or *Aegires punctilucens* (d'Orbigny, 1837) but were *A. pruvotfolae.* The most distinguishing feature of *A. punctilucens* is the "ocular" markings on the dorsum. These markings are not present in Risbec's illustrations or discussion.

Aegires ortizi Templado, Luque, and Ortea 1987

(Figs. 12A–B)

Aegires ortizi Templado, Luque, and Ortea 1987:306, Figs 1–3.

Type material.— Holotype: 15-05/1006, Cayo Bocas de Alonso, Archipelago de los Conerneos, Cuba, Museo Nacional de Ciencias Naturales of Madrid.

Material examined.— Holotype MNCN 15-05/1006, one specimen, 5 mm, Cayo Bocas de Alonso, Archipelago de los Canarreos, Cuba, 4 m, collected April 1984, J. Templado.

Distribution.— *Aegires ortizi* has only been reported from Cuba by the original authors.

Remarks.— Templado et al. (1987) described this species from four specimens collected in 1984 (holotype) and in 1988 (three additional specimens from Cuba). Their description included the external and radular morphology but the reproductive, central nervous system and digestive systems were not described. We were unable to examine the complete reproductive system or nervous system of the holotype, as the specimen appears to have been damaged during the removal of the buccal mass during the original study.

The slide prep of the holotype radula was also examined. Additional material is needed to determine the extent of the pointed denticles on the lateral teeth of *A. ortizi* as described by the original authors.

Aegires palensis Ortea, Luque, and Templado, 1990
(Figs. 16–17)

Aegires palensis Ortea, Luque, and Templado, 1990:336, Figs 1-2.

Type material.— Holotype: 15.05/1035, Cabo de Palos, SE Spain, Museo Nacional de Ciencias Naturales of Madrid.

Material examined.— Holotype MNCN 15.05/1035, one specimen, 6 mm, Cabo de Palos, Bajo de Dentro, Spain, collected July, 1987, J. Templado. MNCN 15.05/27821, one specimen, 2 mm, Aqua Amarga, Spain, 15 m, June 1995, J. Templado.

Distribution.— This species has only been reported from Spain (original description).

External morphology.— Ortea et al (1990) provided a thorough description and drawings of this species. No additional material was available for examination during the present study. However, drawings were made of the preserved paratype (Fig. 16).

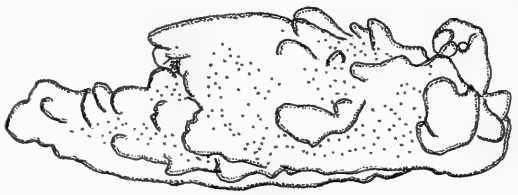


Figure 16. *Aegires palensis* Ortea, Luque, and Templado, 1990. MNCN15.05/1035. Drawing of preserved specimen. Dorsal view. Scale = 0.06 mm.

Reproductive system.— The reproductive system examined here is triaulic (Fig. 17). The ampulla is large and bulbous. It branches into the oviduct and the prostate. The prostate is long and tubular and coils once, then narrows only slightly before entering the long, tubular deferent duct. The deferent duct enters the very wide, long penis. The penis of the specimen was broken off and thus the presence of penial hooks cannot be confirmed. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The short, narrow vaginal duct enters the bursa copulatrix at the proximal end. The receptaculum seminis connects directly to the vaginal duct via a short duct that bifurcates into the oviduct, which leads into the female gland mass. The bursa is nearly round and about two-thirds the size of the ampulla. The receptaculum seminis is ovoid and is approximately one-half the size of the bursa.

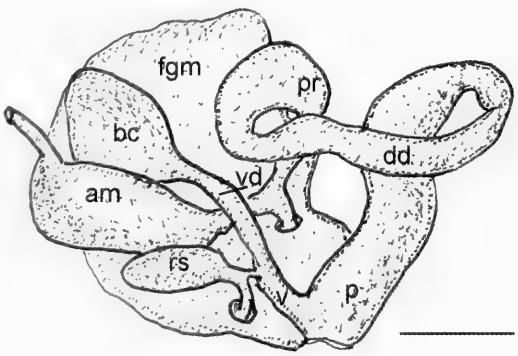


Figure 17. *Aegires palensis* Ortea, Luque, and Templado, 1990. MNCN15.05/1035. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.25 mm.

Central nervous system.— The central nervous system was not available for examination.

Remarks.— Ortea et al. described this species from a single specimen collected in 1987 at 34 m depth from SE Spain. Their description included the external and radular morphologies, but the reproductive, central nervous and digestive systems were not described. A second specimen was deposited into the Museo Nacional de Ciencias Naturales of Madrid in 1995 and examined for the present study. Photo images of specimens collected from the Mediterranean and identified as *A. leuckartii* and *A.* cf. *leuckartii* are most likely *A. leuckartii* and *A. palensis* may be a synonym of *A. leuckartii* (Koehler 2004; Tocino 2004). Additional material of both *A. leuckartii* and *A. palensis* is needed to determine whether this is the case. However, there have been no further reports on

collections or sightings of *A. palensis* except for the two specimens noted herein. No specimens of *A. leuckartii* were available for examination during this study.

Aegires punctilucens (d'Orbigny, 1837)

Polycera punctilucens d'Orbigny, 1837:7, pl 106.
Aegirus punctilucens (d'Orbigny) Alder and Hancock 1845/55, pl. 21.
Aegires hispidus Hesse, 1872:346.
Aegires punctilucens (d'Orbigny) Vayssière 1901:58f.
Aegires punctilucens (d'Orbigny) Pruvot-Fol, 1954:243.

Type material.— Collected (1826) at the Port of Brest, France. No further data are available. Attempts to locate the type material for examination were not successful.

Distribution.— Specimens of *Aegires punctilucens* have been reported from the Atlantic coast of France (d'Orbigny), Scandinavia and the Mediterranean Ocean (Pruvot-Fol 1954).

External morphology.— D'Orbigny provided a thorough accounting of the external morphology of *Aegires punctilucens*. To summarize his description: the body is short but strongly convex, bulged in the middle, slightly tough and covered with flattened tubercles. The tubercles are arranged as follows: two between the rhinophores, four lateral and posterior to these, then one large median and many laterally placed tubercles. There is one large tubercle posterior to the gill, along with four round tubercles placed on each side of the tail median. Around the rhinophores are five elevated tubercles, three larger ones and two very small ones. The foot is elongate, ends in a point and is much narrower than the body, though slightly wider at the median. The gill is tri-lobed and multi-pinnate.

The body color is a mixture of yellow and violet, except in between the tubercles where there are spots of bright green surrounded by a border of black. In front of the gill and between the rhinophores are definite points of matte white, with four smaller points lateral to these. On the foot there are many spots of color, more intense than the rest of the body color, placed obliquely or vertically. The bottom of the foot has a slight border.

Remarks.— Many authors have published descriptions of *Aegires punctilucens*, the species first described by d'Orbigny (1837) as *Polycera punctilucens*. The original description was confined to the external morphology. Subsequent authors (Schmekel and Portmann 1982; Thompson and Brown 1984; Templado et al. 1987) provided more thorough descriptions, including the radular and reproductive anatomy, however none of the previous authors described the central nervous system or circulatory system.

Baba (1974) provided a detailed description of a specimen from Japan, however this specimen is most likely *Aegires exeches* sp. nov. (See the description further on in the present study).

Haefelfinger (1968) synonymized *Aegires leuckartii* with *A. punctilucens*. Schmekel and Portmann (1982) also noted the consistency between these two species, and designated them as subspecies. Thompson's publication (1984) maintained the synonymy of the two (see discussion under *A. albopunctatus*).

As stated previously, there is no description of the reproductive morphology from the original material. Due to this lack, and the differences in the external morphology between *A. punctilucens*, *A. leuckartii* and *A. albopunctatus* and considering Schmekel and Portmann's argument for separate subspecies, we propose to maintain *A. punctilucens* from the Mediterranean Sea as a separate species from *A. leuckartii* and *A. albopunctatus*.

Aegires sublaevis Odhner, 1932

(Figs. 18–25)

Aegires sublaevis Odhner, 1932:39.
Serigea sublaevis (Odhner) Nordsieck, 1972:55.

Type material.— Puerto de Orotavo, Tenerife, Canary Islands.

Material examined.— CASIZ 168921, four specimens, one specimen, 10 mm, dissected, Ponta de Piramede, Azores, no depth available, collected July 1988, T. Gosliner. CASIZ 078393, one specimen, 8 mm, dissected, Punta Cormorant, Isla Floreana, Galápagos Islands, no depth available, collected September 1991, T. Gosliner. CASIZ 072608, three specimens, one specimen, 5 mm, dissected, Ila São Miguel, 1 km E of Caloura, Azores, 20 m, collected July 1988, T. Gosliner. CASIZ 072603, one specimen, 9 mm, Ila São Miguel, Mosteiros, Azores, 3 m, collected July 1988, T. Gosliner. CASIZ 168923, three specimens; one specimen, 12 mm, dissected. Ponta de Galora, Azores, collected July 1988, T. Gosliner.

Distribution.— This species has been reported from the Mediterranean Sea (Schmekel and Portmann 1982); the Canary Islands (Odhner 1932; Altimira and Ros 1979; Pérez Sánchez, Bacallado and Ortega 1991; Ortea et al. 1996; Ortea et al. 2000)); Panama (Meyer 1977), Bermuda (Thompson 1981) and the Galápagos Islands, which represents the first record from the Pacific (present study).

External morphology.— The external morphology of this species has been described extensively in the literature (Odhner 1932; Meyer 1977; Altimira and Ros 1979; Thompson 1981; Schmekel and Portmann 1982; Templado et al. 1987) and will not be repeated here. However, drawings were made of preserved specimens from the Azores to compare to specimens from the type locality (Fig. 18). These specimens match Odhner's original description. We noted one differ-

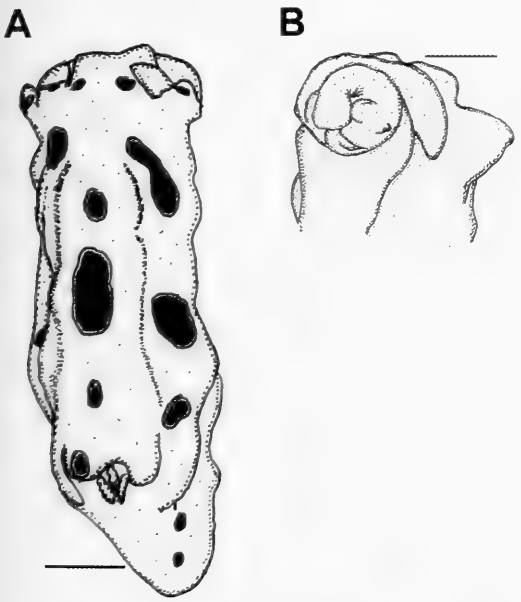


Figure 18. *Aegires sublaevis* Odhner, 1932. CASIZ 168921. Drawing of preserved specimen: (A) Dorsal view. (B) Ventral view of head. Scale = 1.43 mm.

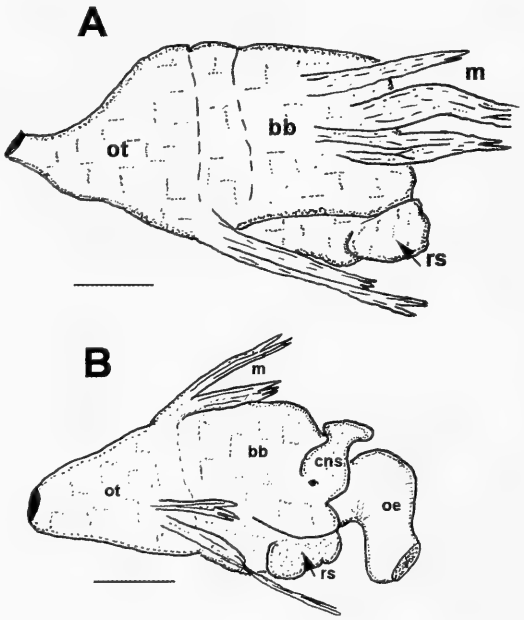


Figure 19. *Aegires sublaevis* Odhner, 1932. Buccal bulbs: (A) CASIZ 072608. (B) CASIZ 078393, bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, ot = oral tube, rs = radular sac, scale = 0.33 mm.

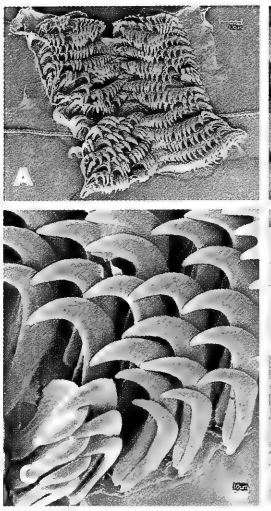


FIGURE 20. *Aegires sublaevis* Odhner, 1932. CASIZ 072608. Buccal morphology: (A)Whole radula, scale = 100 μm. (B) Inner lateral teeth, scale = 10 μm. (C) Outer lateral teeth, scale = 10 μm. (D) Jaw, scale = 20 μm.

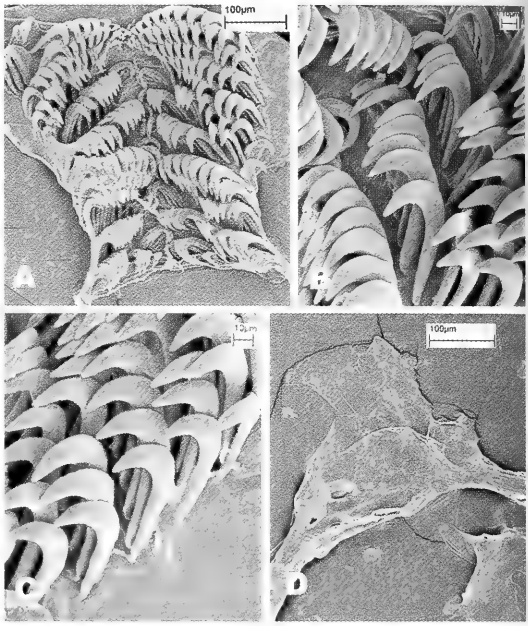


FIGURE 21. *Aegires sublaevis* Odhner, 1932. CASIZ 078393. Buccal morphology: (A) Whole radula, scale = 100 μm. (B) Inner lateral teeth, scale = 10 μm. (C) Outer lateral teeth, scale = 10 μm. (D) Jaw, scale = 100 μm.

ence between specimens examined from the Azores and those from the Galápagos Islands. Specimens from the Azores have one ring of dark pigment on the rhinophores whereas those from the Galápagos have two dark rings.

DIGESTIVE SYSTEM.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is rounded and the radular sac protrudes noticeably from the posterior side (Fig. 19). There were no oral glands noted. The radular formula is 17 × 17.0.17 for a 12 mm specimen from the Azores (CASIZ 168921)(Fig. 20) and 12 × 13.0.13 for an 8 mm specimen from the Galápagos (CASIZ 078393) (Fig. 21). The jaw is well developed and has a thickened edge. No labial rods were noted (Figs. 20D, 21D). All teeth are simply hamate, with a pointed hook. Rachidian teeth are absent. The first inner lateral tooth is much smaller than the remaining lateral teeth. The next two lateral teeth are slightly larger than the first lateral tooth. The outermost lateral tooth is shorter than the middle teeth.

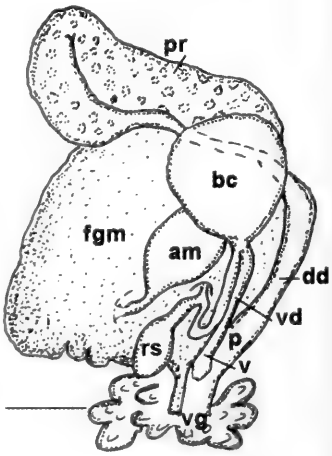


FIGURE 22. *Aegires sublaevis* Odhner, 1932. CASIZ 168921. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, vg = vestibular gland, scale = 0.33 mm.

REPRODUCTIVE MORPHOLOGY.— The reproductive morphology of the specimens examined for the present study (Figs. 22–24) closely resembles the drawings and descriptions previously reported by Schmekel and Portmann (1982).

The reproductive system is triaulic. The ampulla is large and bulbous. It branches into the oviduct and the prostate. The prostate is long and tubular and coils twice, then narrows for a short distance before entering the wider deferent duct. The deferent duct enters the long penis, which is wider than the deferent duct. The penis has small densely packed penial hooks that extend

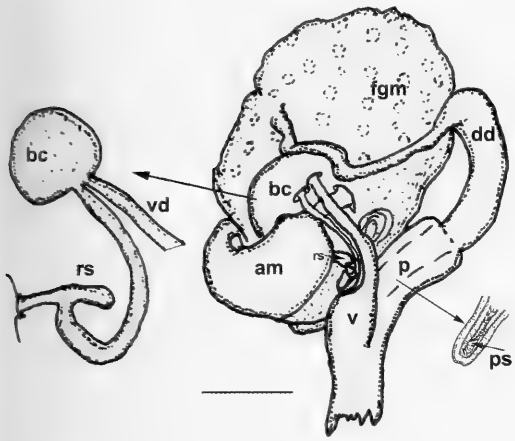


FIGURE 23. *Aegires sublaevis* Odhner, 1932. CASIZ 072608. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.5 mm. [NB. Vestibular gland not evident.]

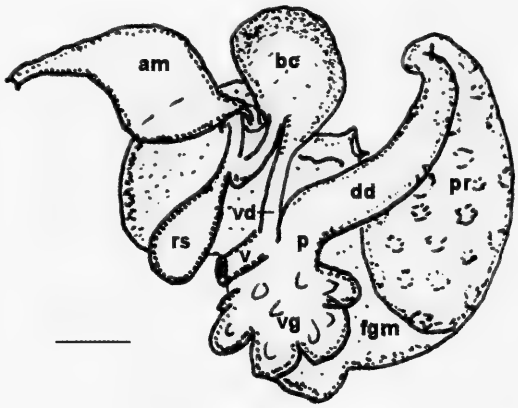


FIGURE 24. *Aegires sublaevis* Odhner, 1932. CASIZ 078393. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, vg = vestibular gland, scale = 0.5 mm.

throughout the length of the penis. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The long, narrow vaginal duct enters the bursa copulatrix at the proximal end. The receptaculum seminis connects to the bursa with a longer duct than the oviduct, which leads from the bursa into the female gland mass. The bursa is round and as large as the ampulla. The receptaculum seminis is ovoid and less than one-half the size of the bursa. Specimens examined have a vestibular gland at the genital atrium (Figs. 22 and 24) as described by Schmekel and Portmann. However, in the specimen examined from the Azores, the vestibular gland was not evident. It may have broken off. No other *Aegires* species has this gland.

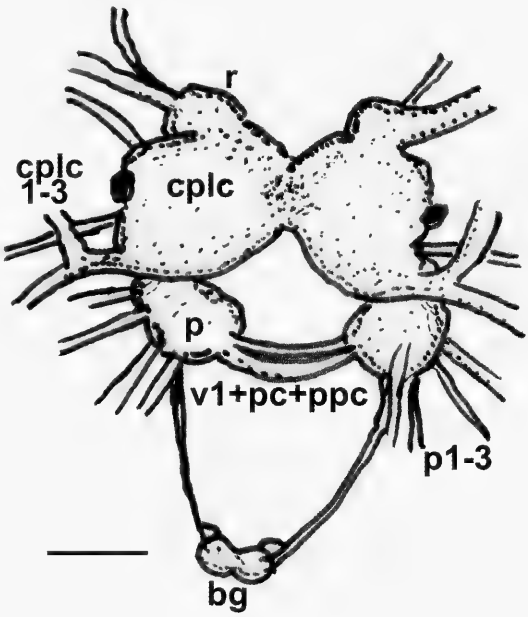


FIGURE 25. *Aegires sublaevis* Odhner, 1932. CASIZ 072608. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.2 mm.

CENTRAL NERVOUS SYSTEM.— The central nervous system has fused cerebral and pleural ganglia (Fig. 25). The eyes are small and sessile on the cerebral-pleural complex, but protrude slightly at the sides of the cerebral-pleural complex. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

Remarks.— The specimen from the Galápagos represents the first record of this species from the Pacific. With the exception of having two pigment rings on each rhinophore, Galápagos specimens are identical to Atlantic specimens of *A. sublaevis*.

Odhner's (1932) description of *Aegires sublaevis* is quite detailed but did not include a description of the reproductive system. However, Schmekel and Portmann (1982) provided a complete description of the reproductive anatomy in their thorough study. Templado et al. (1987) described the external and radular morphology of this species. In both these studies, drawings of the examined features accompany the description.

Nordsieck (1972) established a new genus *Serigea* and designated *S. sublaevis* (Odhner, 1931) (with an incorrect date cited) as the type species. He placed *Serigea* in the Family Aegiretidae based on similar characters to *Aegires*. He described the following *Serigea* characters: dorsal papillae, smooth rhinophores, gill with protective valves, among others. However, Nordsieck did not indicate why a new genus was needed for these characters. Altimira and Ros (1978) published a study on the molluscs of the Canary Islands, declaring that *Serigea* equals *Aegires sublaevis* Odhner. Subsequent publications on *Aegires sublaevis* also recognized this name exclusively (Meyer 1977; Thompson 1981; Schmekel and Portmann 1982; Templado et al. 1987).

Aegires villosus Farran, 1905

(Figs. 26–27)

Aegires villosus Farran, 1905:329-364, pls 1–6.
Aegires spp. Debelius, 1996:192, bottom large photo. Misidentification.

Type material.— Collected from the northwest of Cheval Paar, Ceylon.

Material examined.— CASIZ 158799, one specimen, 5 mm, dissected. Luzon, Batangas, Philippine Islands, collected 6 May 2001, T. Gosliner. CASIZ 088089, one specimen, 12 mm, dissected. Layag Layag, Batangas, Philippine Islands, collected 27 March 1993, T. Gosliner. CASIZ 105658, one specimen, 8 mm, dissected. Kirby's Rock, Batangas, Philippine Islands, collected 23 February 1995, T. Gosliner. CASIZ 65306, one specimen, 6 mm, Madang, Papua New Guinea, collected 22 January 1988, R. Willan. CASIZ 116888, one specimen, 12 mm, dissected. Coral Ledge, Garden Island, Western Australia, collected 6 January 1999, S. Fahey.

Distribution.— *Aegires villosus* has been reported from Ceylon (Farran 1905), Japan (Baba 1955), New Caledonia (Risbec 1928), Dar es Salaam, Tanzania (Edmunds 1971), Papua New Guinea (present study), Bali, Malaysia, Samoa and Australia (Rudman 2004).

External morphology.— Several authors have described and/or drawn this species (Farran 1905; Risbec 1928; Baba 1955; Edmunds 1971; Rudman 2004). The specimens examined for the present study from various localities match the existing drawings and descriptions of the external morphology of *Aegires villosus* and no additional detail is necessary.

Digestive system.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is ovoid and the large radular sac does not protrude noticeably from the posterior-ventral side (Fig. 26). There are numerous ovoid oral glands that cover the sides of the oral tube near the mouth and line the posterior edge of the oral tube. Two tubular salivary glands extend from the underside of the esophagus and lie along the top of the buccal bulb. The radular morphology was described by previous authors and the present study (Fig. 26) confirms the morphology as described by Farran (1905) and Risbec (1928). Edmunds (1971) described the outer lateral tooth as being elongate, but we did not find this to be the case. The radular formula for the 12 mm specimen dissected is 16 × 17.0.17. All teeth are simply hamate, with the innermost tooth being substantially smaller than the remaining teeth in each row. The second

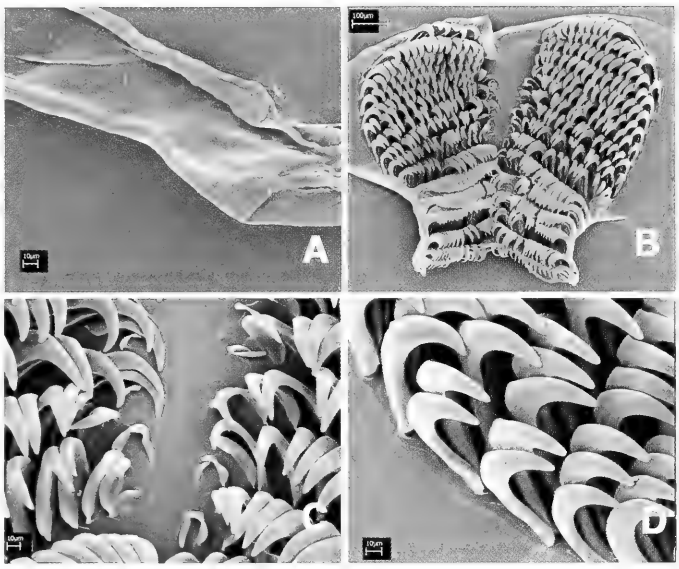
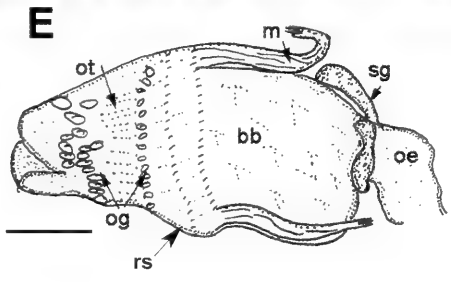
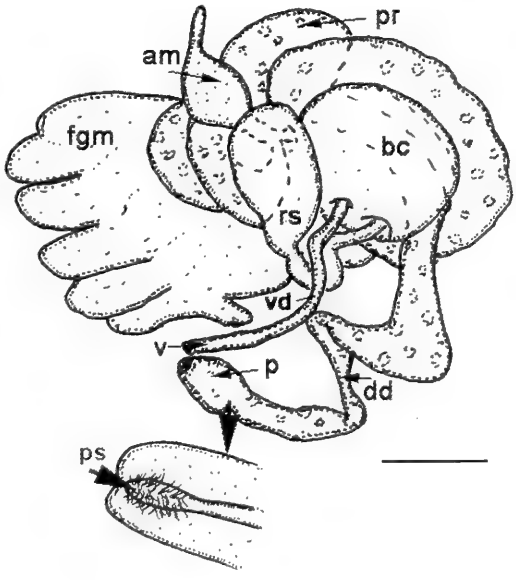


FIGURE 26. *Aegires villosus* Farran, 1905. CASIZ 088089. Buccal morphology: (A) Jaw, scale = 10 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm. (E) Buccal bulb, bb = buccal bulb, m = muscle, oe = esophagus, og = oral glands, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.25 mm.

lateral tooth is also reduced in size.

REPRODUCTIVE SYSTEM.— The reproductive morphology has not been thoroughly described previously. The reproductive system is triaulic. The ampulla is small and ovoid. It branches into a short oviduct and the prostate (Fig. 27). The oviduct enters the female gland mass near an edge. The prostate is a very long, thick, coiled tube. It narrows slightly before widening slightly into the ejaculatory duct and terminates at a slightly bulging penis. There are small hooks inside the penis located at the distal end only. The vagina is long and narrow. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At its proximal end it joins the bursa copulatrix. A long separate duct joins the large ovoid receptaculum seminis to the base of the bursa, and also connects to the female gland mass. The bursa is large, spherical and the receptaculum seminis is over half the size of the bursa.





CENTRAL NERVOUS SYSTEM. The central nervous system is as found in other *Aegires* species. That is, it has fused cerebral and pleural ganglia (not shown). The eyes are large and sessile on the cerebral-pleural complex and do not protrude. The pedal ganglia are slightly

FIGURE 27. *Aegires villosus* Farran, 1905. CASIZ 088089. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

Remarks.— Farran (1905) described *Aegires villosus* from one specimen collected from Cheval Paar, Ceylon (Sri Lanka). The description included the external morphology and radular morphology, along with adequate drawings of each. Other authors provided further details of the external anatomy, radular morphology, the central nervous system and/or the reproductive system (Edmunds 1971; Risbec 1928). Except for one difference, the specimens examined for the present study matched the previous descriptions in both external and internal morphology. Edmunds illustrated and described elongate outer radular teeth in the 4 mm specimen he examined. He also stated that the outermost tooth was very small and not illustrated in this immature specimen. The larger 8 mm specimen that he collected was not illustrated. The 8 and 12 mm specimens that we examined had simply hamate outer lateral teeth.

New Species Descriptions

Family Aegiridae Fischer, 1883

Genus *Aegires* Lovén, 1844

***Aegires ninguis* Fahey and Gosliner, sp. nov.**
(Figs. 1D, 28–32)

=*Aegires* sp. Gosliner, 1987:99, top photograph

Type material.— Holotype: CASIZ 073982, one specimen, 6 mm, Phillip's Reef, Algoa Bay, Cape Province, Indian Ocean, South Africa, 10 m, collected January 1991, T. Gosliner. Paratypes: CASIZ 073230, six specimens, 4–6 mm, Phillip's Reef, Cape Province, Indian Ocean, South Africa, 10 m, collected May 1984, T. Gosliner. CASIZ 073929, one specimen, 8 mm, dissected, Llandudno, Cape Province, Atlantic Ocean, South Africa, 23 m, collected October 1982, T. Gosliner. A35568, one specimen, 6 mm, Miller's Point, Indian Ocean, South Africa, 8 m, collected June 1980, T. Gosliner. A35569, one specimen, 8 mm, Bakoven, Atlantic Ocean, South Africa, 15 m, collected September 1982, T. Gosliner.

Distribution.— This species has only been reported from the temperate Atlantic and Indian Oceans of South Africa (present study).

Etymology.— The specific name *ninguis* is Latin, meaning snowy, which describes the appearance of the dorsum with the white background and tiny opaque white speckles.

External morphology.— The body shape is ovoid, slightly raised and has a rounded posterior end of the foot that extends only slightly (Fig. 1D). There is a slightly pronounced oral veil that has a scalloped edge (Fig. 28). The dorsum is covered with short, rounded tubercles, all with rounded tops. There are no tubercles on the posterior end of the foot. There are two prominent tubercles on the anterior of the head region, with smaller tubercles between them, and two prominent tubercles on the poste-

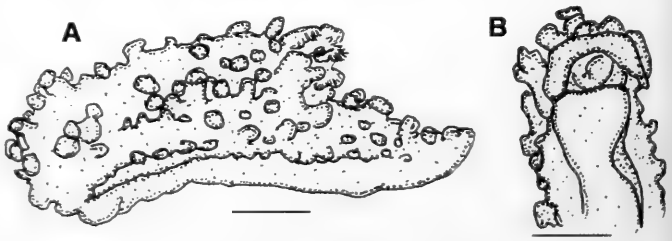


Figure 28. *Aegires ninguis* sp. nov. CASIZ 073982. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 1.5 mm.

rior of the dorsum that appear joined together. There are also two prominent tubercles between the rhinophores with smaller tubercles between them. Numerous spicules protrude from the tops of the tubercles giving a fuzzy appearance. The rhinophore sheath is only slightly elevated but has five papillae, 3 large and 2 small, on all sides except the innermost. The rhinophores are smooth. The gill pocket lies at the posterior third of the dorsum and is protected on the anterior side by extra-branchial papillae that are tri-lobed. The three small gill branches are bipinnate.

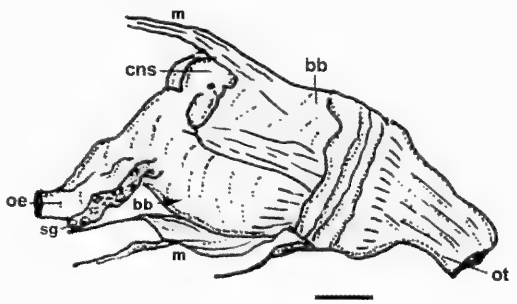


FIGURE 29. *Aegires ninguis* sp. nov. CASIZ 073929. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 0.25 mm.

The background color is white to pale yellow. There are minute white speckles on the dorsum, between the tubercles. There are no additional colors found on the specimens examined. The rhinophores are pale yellow on white specimens and deeper yellow on the yellow specimens. The gill matches the background color of the living animal.

DIGESTIVE SYSTEM.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is rounded and the radular sac barely protrudes from the posterior side (Fig. 29). There are two short salivary glands situated beneath the esophagus. There were no oral glands noted. The radular formula is 17 × 16.0.16 for a 8 mm specimen (Fig. 30). The jaw (Fig. 30A) is well developed and has a thickened edge with narrow rod-like elements. All teeth are simply hamate, with pointed hooks. Rachidian teeth are absent. The four inner lateral teeth are smaller than the remaining lateral teeth. The outermost lateral teeth are shorter than the middle teeth.

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 31). The ampulla is short but very wide and branches into the oviduct and the prostate. The prostate is a long, thick tube and narrows only very slightly before entering the long, wide penis. The penis, which expands at the genital atrium, has small densely packed hooks only at the distal end. The vagina is long and wide. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the short, wide vaginal duct enters the bursa copulatrix. The receptaculum seminis connects directly to the vagina via a short duct. The oviduct, connected to the

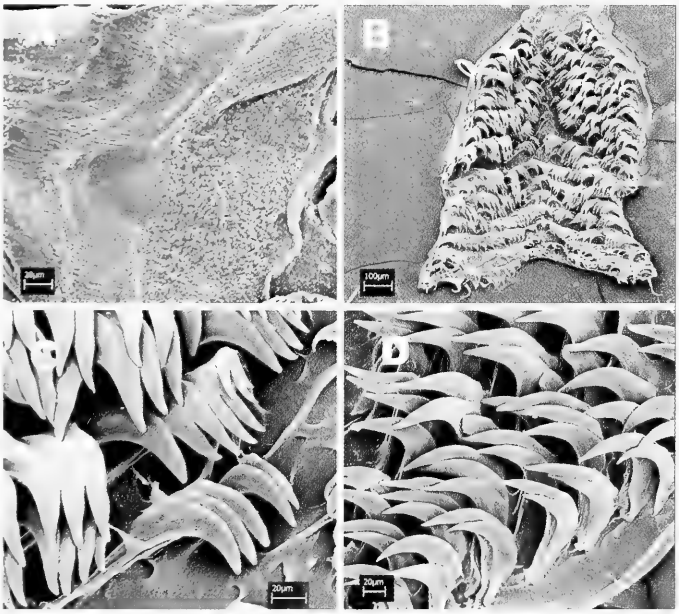


FIGURE 30. *Aegires ninguis* sp. nov. CASIZ 073929. Buccal morphology: (A) Jaw, scale = 20 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 20 µm.

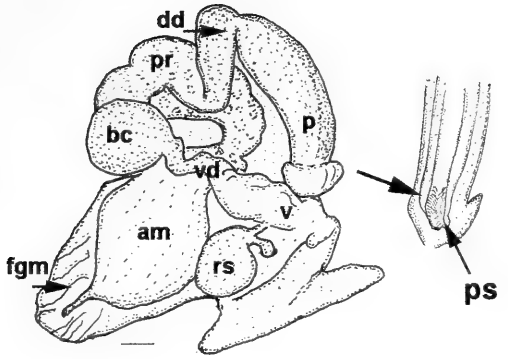


FIGURE 31. *Aegires ninguis* sp. nov. CASIZ 073929. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.33 mm.

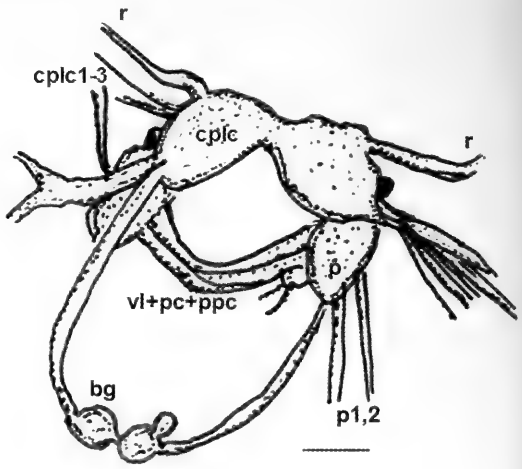


FIGURE 32. *Aegires ninguis* sp. nov. CASIZ 073929. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.14 mm.

receptaculum, enters the female gland mass. The bursa is round and slightly larger than the round receptaculum seminis.

CENTRAL NERVOUS SYSTEM.— The central nervous system has fused cerebral and pleural ganglia (Fig. 32). The eyes are small and sessile on the cerebral-pleural complex, but protrude slightly at the sides of the cerebral-pleural complex. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

CIRCULATORY SYSTEM.— (not pictured) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

REMARKS.— Externally, the white form of *Aegires ninguis* most closely resembles the white form of *A. albopunctatus*. Although neither color form (white or pale yellow) of *A. ninguis* has been found with dark spots on the dorsum, both forms do have minute white dots covering the dorsum as is found on *A. albopunctatus*. Both *A. ninguis* and *A. albopunctatus* have yellow rhinophores. The tubercle arrangement is different between these two species. *Aegires ninguis* has randomly scattered tubercles that vary in size on the notum. There are two prominent tubercles on both the anterior and posterior ends of the notum. There are no tubercles on the posterior end of the foot. In *A. albopunctatus* the tubercles are arranged in two distinct rows like ridges, joined from between the rhinophores and extending to the gill. Behind the gill, the tubercles are arranged in three distinct rows (MacFarland 1966). The tubercles on the rhinophore pocket of each species are different as well. In *A. ninguis*, there are four tubercles on the outside rhinophore pocket and in *A. albopunctatus* there are five.

The gill morphology differs between the two species. *Aegires ninguis* has very small gill leaves that are almost completely covered by the large, flat-topped protective tubercles. *Aegires*

albopunctatus has larger gill leaves that protrude vertically with a branching lobe protecting each plume (MacFarland 1966: plate 18).

Internally, the two species also differ. The most noticeable difference in the reproductive morphology is that in *A. ninguis* the receptaculum seminis connects directly to the vagina via a short oviduct. In *A. albopunctatus* the receptaculum connects to the bifurcating oviduct at the base of the bursa copulatrix and to the female gland mass. Also, *A. albopunctatus* has spines throughout the penis while in *A. ninguis* the spines are just at the apex.

The deferent duct of these two species differs markedly. In *A. ninguis* the deferent duct is short and tubular. In *A. albopunctatus* the duct is very long, thin and coiled. The penis of *A. ninguis* is very tubular and long, while that of *A. albopunctatus* is much smaller relative to the other reproductive organs such as the vagina and the bursa.

No other species of *Aegires* has the particular combination of characters displayed by *A. ninguis*. The most externally similar species, *Aegires albopunctatus* is found along the Eastern Pacific while *A. ninguis* has been found only in South Africa.

Aegires lemoncello Fahey and Gosliner, sp. nov.

(Figs. 1E, 33–37)

= *Aegires* sp. 2, Valda Fraser, 2000 and Rudman in SeaSlug Forum.

Type material.— Holotype: CASIZ 086465, one specimen, 4 mm, dissected, Barracuda Point, Pig Island, Madang, Papua New Guinea, 9 m, collected June 1992, T. Gosliner.

Distribution.— This species has only been reported from Papua New Guinea (present study), South Africa (photo, V. Fraser) and Eastern Australia (no photo, B. Rudman).

Etymology.— The specific name *lemoncello* is from the Italian liqueur of the same color as some specimens of this new species.

External morphology.— The body shape is elongate, slightly raised and has a very narrow posterior (Fig. 1E). The dorsum has elongate papillae with flattened tops. Spicules protrude from the tops of the tubercles. The extended oral veil has 10–11 rounded tubercles on the dorsal surface (Fig. 33). The rhinophore sheath is slightly elevated, smooth and protected by a single elongated papilla on the outer edge. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and is protected on the anterior side by five elongate papillae that project posteriorly. Posterior to the gill are two small papillae near the center-line. The three small gill branches are bipinnate.

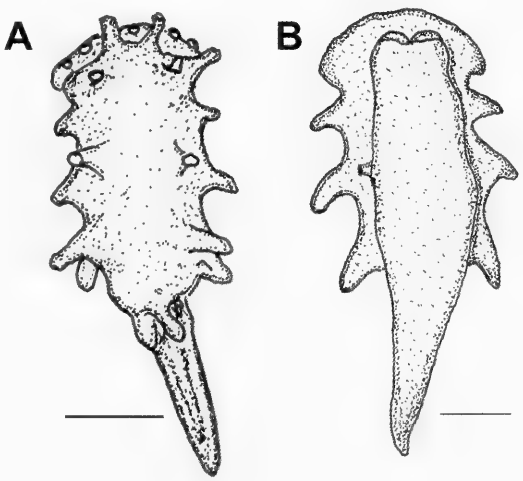


Figure 33. *Aegires lemoncello* sp. nov. CASIZ 086465. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view. Scale = 2.25 mm.

The background color is pale yellowish white to creamy yellow. The papillae are deeper yellow, with a single ring of orange approximately half way along the length. The rhinophores are the same deeper yellow as the papillae. The gill branches are pale yellow.

Digestive system.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is round and the radular sac barely protrudes from the

posterior side (Fig. 34). There are two elongate salivary glands situated beneath the esophagus. There were no oral glands noted. The radular formula is 13 × 15.0.15 for a 4 mm specimen. The jaw is well developed and has a thickened edge (Figs. 34B, 35). All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The three inner lateral teeth are much thinner and less hooked than the remaining lateral teeth. The outer lateral teeth have a short hook.

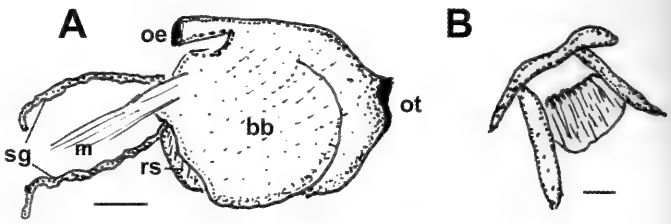


FIGURE 34. *Aegires lemoncello* sp. nov. CASIZ 086465. (A) Buccal bulb: bb = buccal bulb, m = muscle, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary gland, scale = 0.5 mm. (B) Labial cuticle, scale = 0.05 mm.

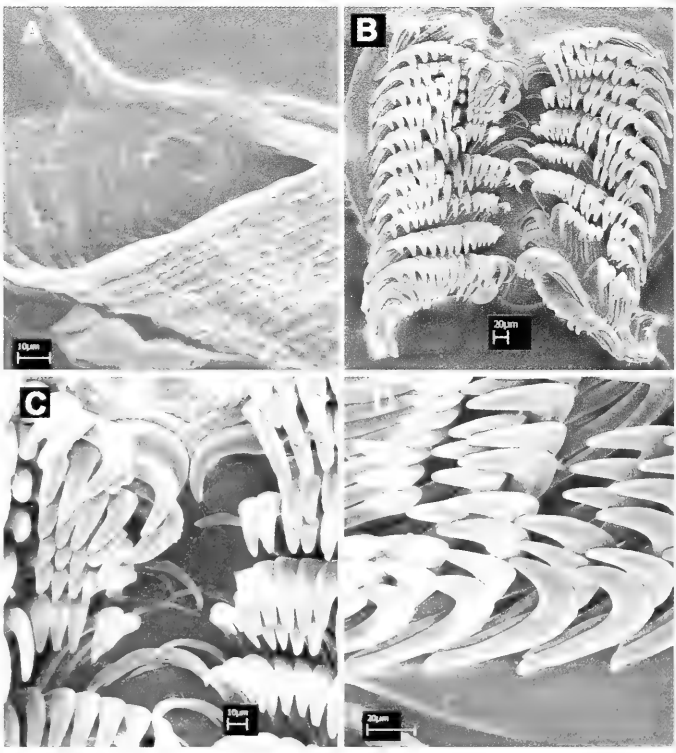


FIGURE 35. *Aegires lemoncello* sp. nov. CASIZ 086465. Buccal morphology: (A) Jaw, scale = 10 µm. (B) Whole radula, scale = 20 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 20 µm.

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 36). The ampulla is elongate and branches into the oviduct and the prostate. The prostate is long and tubular and narrows slightly before entering the elongate deferent duct. The deferent duct widens only slightly, then enters the short, wide penis. The penis has small densely packed penial hooks at the distal tip only. The vagina is much narrower than the penis. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the long, narrow vaginal duct enters the bursa copulatrix. The receptaculum seminis connects to the bursa with a separate long duct that bifurcates into the oviduct, which enters the female gland mass. The bursa is ovoid and approximately the same size as the ovoid receptaculum seminis.

CENTRAL NERVOUS SYSTEM.— The central nervous system has fused cerebral and pleural ganglia (Fig. 37). The eyes are large and sessile on the cerebral-pleural complex, but protrude slightly at the sides of the cerebral-pleural complex. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

CIRCULATORY SYSTEM.— (not shown) The heart is relatively small as compared to most cryp-

tobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Externally, *Aegires lemoncello* does not resemble any other *Aegires* species. Although *A. lemoncello* has elongate tubercles like *Aegires villosus*, the tubercles in that species are more numerous and more complex especially around the rhinophores where there are 4–5 tubercles on a raised pocket. The tubercles of *A. lemoncello* look more like soft papillae, and there is only one tubercle that lies at the outer side of the rhinophores. The color of these two species is not similar at all. *Aegires lemoncello* has a yellow or whitish background color with orange rings around the rhinophores and tubercles. *Aegires villosus* has a white body color with purple and yellow irregular markings covering the notum.

Internally, the morphological characters also set this species apart from other *Aegires*. *Aegires lemoncello* has three elongate curved inner lateral teeth, a feature found in other *Aegires* (*A. ortizi* and *A. petalis*). *Aegires pruvotfolae* has one elongate inner lateral tooth while both *A. ortizi* and *A. petalis* have two. Neither of these species even closely resembles *A. lemoncello* externally, either in color or tubercle morphology.

The reproductive morphology also sets *A. lemoncello* apart from other *Aegires*. The combination of a long, thin deferent duct leading from a narrow prostate and into a slightly wider penis is not found in other *Aegires*. The species that most closely matches this anatomy, *A. hapsis*, does not share any other internal or external characters. The large ovoid receptaculum that enters the common oviduct at the base of the bursa copulatrix is different from other *Aegires* species also. The receptaculum of other *Aegires* species either enters a common oviduct with the bursa, or enters the vaginal duct or into the vagina directly (*A. ninguis*).

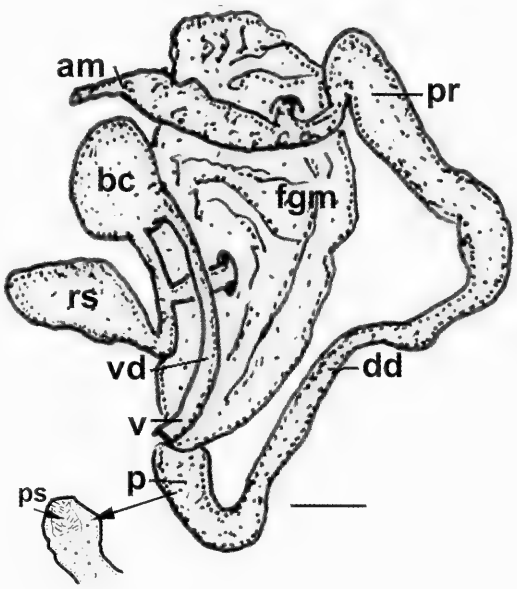


Figure 36. *Aegires lemoncello* sp. nov. CASIZ 086465. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

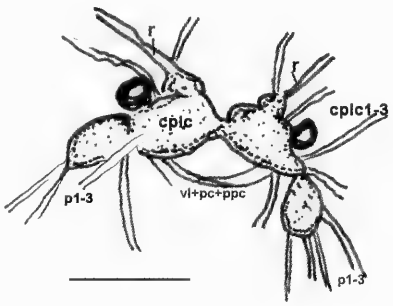


Figure 37. *Aegires lemoncello* sp. nov. CASIZ 086465. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, cl+pc+ppc = visceral loop, scale = 0.25 mm.

The combination of characters exhibited by *Aegires lemoncello* sets it apart as a previously undescribed species of *Aegires*.

Aegires malinus Fahey and Gosliner, sp. nov.

(Figs. 1F, 38–42)

Type material.— Holotype: CASIZ 085889, one specimen, 8 mm, Bebbit, Batangas Region, Philippines, collected March 1993, T. Gosliner. Paratypes: CASIZ 168919, one specimen,

15 mm, dissected, Bebbit, Philippines, collected March 1993, T. Gosliner. CASIZ 096248, one specimen, 14 mm, Layag-Layag, Batangas Region, Philippines, collected March 1994, M. Miller.

Distribution.— This species has only been reported from the Philippine Islands (present study).

Etymology.— The specific name *malinus* is Latin for apple green, the color of the rhinophore and gill appendages of this species.

External morphology.— The body shape is elongate and convex. There are tiny pointed, randomly scattered tubercles on the dorsum (Figs. 1F, 38). The rhinophore pockets are raised and the outer edge is taller with 3 flat-topped tubercles of varying size and a lobed frill that resembles tufts of seaweed. The rhinophores are smooth. The gill pocket is protected by 3 tall, flat tubercles. The gill leaves are feathery, resembling tufts of seaweed and are multi-pinnate. They extend beyond the protective tubercles.

The background color of the dorsum is deep reddish-brown. The raised rhinophore pocket is the same as the background color and the lobed frill and tubercles are apple green. The rhinophores are white with concentric bands of brown speckles around the club. The gill leaves are pale yellowish-green and the protective tubercles are bright apple green.

Digestive system.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is elongate and the large radular sac protrudes noticeably from the posterior-ventral side (Fig. 39). There are numerous ovoid oral glands that extend from the ventral side of the oral tube. Two short salivary glands extend from the underside of the esophagus. The jaw is well developed and has a thickened edge with long rods along the edge (Fig. 40A). The radular formula for a 15 mm specimen is 22 × 8.0.8 (Fig. 40). The teeth are simply hamate, and the 3–5 innermost teeth much smaller and thinner than the remaining teeth. Rachidian teeth are absent. The outermost teeth are larger than the middle lateral teeth.

Reproductive system.— The reproductive system is triaulic (Fig. 41). The ampulla is very long and tubular. It branches into the oviduct and the prostate. The tubular prostate is approximately the same length as the ampulla and it coils once before narrowing into the thin, elongate deferent duct. The deferent duct is very long and widens slightly, then enters the long penis. The penis is wider than the deferent duct and it has small densely packed hooks at

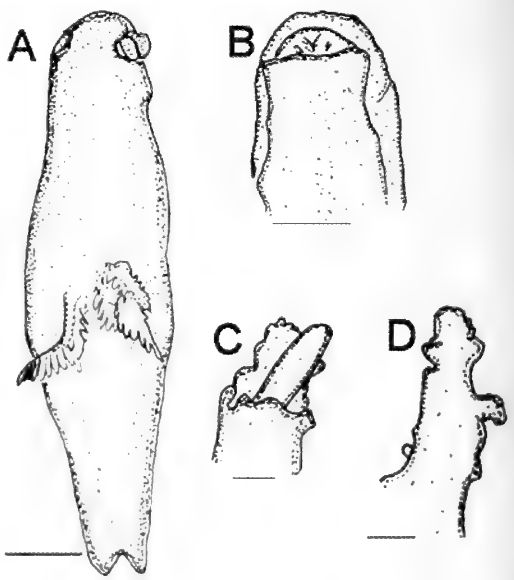


Figure 38. *Aegires malinus* sp. nov. CASIZ 085889. Drawing of preserved animal. (A) Dorsal view, scale = 1.88 mm. (B) Ventral view of head, scale = 1.88 mm. (C) View of rhinophore pocket from inner edge, scale = 0.5 mm. (D) View of rhinophore pocket from outer edge, scale = 0.5 mm.

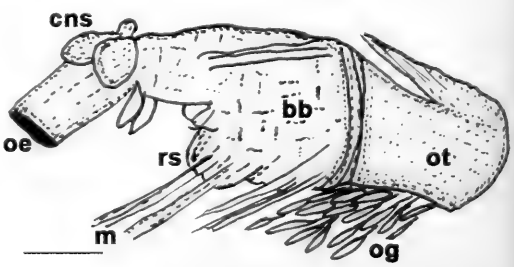


Figure 39. *Aegires malinus* sp. nov. CASIZ 168919. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, og = oral glands, ot = oral tube, rs = radular sac. scale = 0.4 mm.

the distal tip only. The vagina is narrower than the penis. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the long, narrow vaginal duct enters the bursa copulatrix. The receptaculum seminis connects to the bursa via a separate longer duct that bifurcates into the oviduct, which enters the female gland mass. The bursa is ovoid and slightly smaller than the ovoid receptaculum seminis.

Central nervous system.— The central nervous system has fused cerebral and pleural ganglia (Fig. 42). The eyes are large and sessile on the cerebral-pleural complex and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

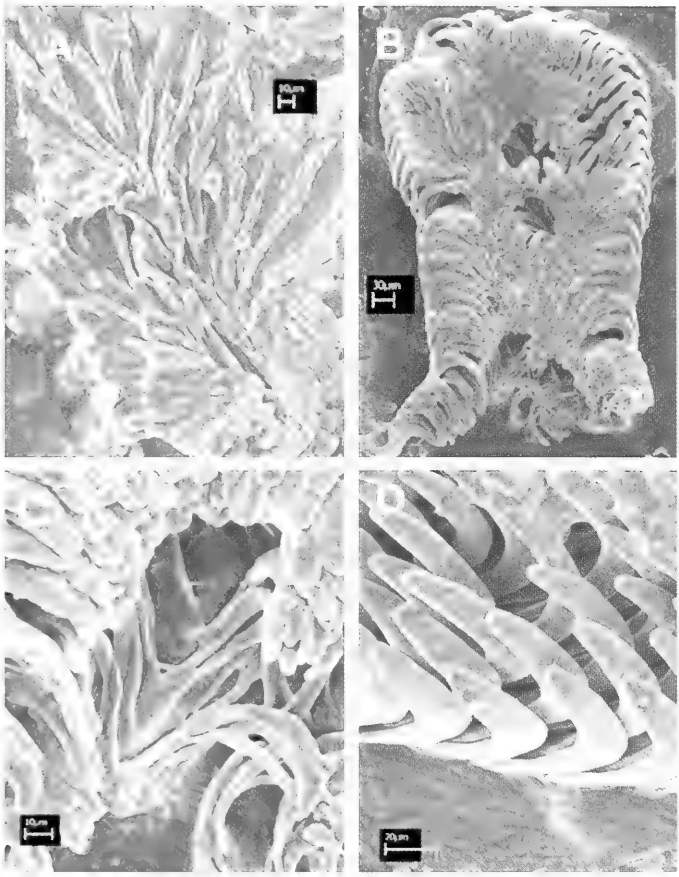


Figure 40. *Aegires malinus* sp. nov. CASIZ 168919. Buccal morphology: (A) Jaw rodlets, scale = 10 μm. (B) Whole radula, scale = 30 μm. (C) Inner lateral teeth, scale = 10 μm. (D) Outer lateral teeth, scale = 20 μm.

Circulatory system.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Externally, *Aegires malinus* does not resemble any other *Aegires* species in either color or body texture. Along with *A. hapsis,* it is one of the two *Aegires* species that does not have prominent dorsal tubercles. However, like other *Aegires*, the rhinophore pockets are lobed, particularly on the outer edge. But the lobes are distinctly different from the texture of the notum. The gill is also protected by appendages, as with other *Aegires*,

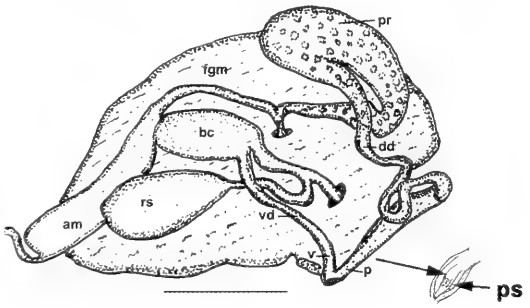


Figure 41. *Aegires malinus* sp. nov. CASIZ 168919. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.86 mm.

but in *A. malinus* the appendages are tall, narrow, yet shorter than the gill leaves. This is unusual for *Aegires*, in which the gill is normally small and almost hidden by the appendages.

Internally, *A. malinus* shares some reproductive characters with other *Aegires* species, such as a bursa and receptaculum that are nearly equal in size, a tubular coiled prostate and an elongate penis with spines. The ampulla in *A. malinus* is extremely elongate, as is found in *A. petalis*. But in *A. petalis*, the penial morphology is different, in that the penis is very short and wide as compared to *A. malinus*, in which it is elongate. Externally, these two species share no common features or color.

Aegires malinus has numerous oral glands clustered at the base of the oral tube. *Aegires villosus* also has clustered oral glands, but in that species the glands are more numerous and there is a second row of glands along the oral tube (see Fig. 26). The other species in which oral glands were observed are *A. incusus* and *A. hapsis*. But the glands in those two species have a different morphology (see Figs. 44 and 63).

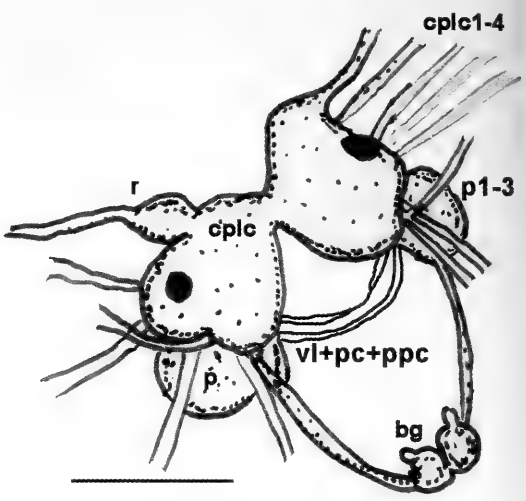


FIGURE 42. *Aegires malinus* sp. nov. CASIZ 168919. Central nervous system: bg = buccal ganglia, cplc = cerebropleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.3 mm.

The particular combination of characters sets *Aegires malinus* apart as a new, previously undescribed species.

Aegires incusus Fahey and Gosliner, sp. nov.

(Figs. 1G, 43–47)

Aegires citrinus Nakano, 2004:117, no. 242, bottom left photograph. Misidentification.
= *Aegires* sp. 1 Rudman, 2004, leading photo for *Aegires* in SeaSlug Forum.

TYPE MATERIAL.— HOLOTYPE: CASIZ 070357, one specimen, 4 mm. Patch Reef, Mora Mora, Tulear, Madagascar, collected April 1989, T. Gosliner. PARATYPES: CASIZ 156668, one specimen, 5 mm, dissected, Cemetary Beach, Maricaban Island, Luzon, Philippines, 0.5 m, collected May 2001, Y. Camacho.

DISTRIBUTION.— This species has only been reported from Madagascar, Philippine Islands (Rudman 2004 and present study) and from Japan (Nakano 2004).

ETYMOLOGY.— The specific name *incusus* is taken from the Latin word meaning anvil, the shape of many of the tubercles of this new species.

EXTERNAL MORPHOLOGY.— The body shape is elongate and slightly rounded (Fig. 1G). There is no obvious oral veil as is found in other *Aegires* species. The posterior third of the body is much narrower than the rest of the body. The dorsum has tall, anvil or mushroom-shaped tubercles with flat tops. There are smaller tubercles along the edge of the posterior end of the foot and one prominent tubercle on the tip. Spicules protrude from the tops of all tubercles. The rhinophore pocket is slightly elevated and is usually surrounded by three tubercles that vary in size. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and three tubercles protect the anterior side of the gill pocket. The small gill leaves are bipinnate.

The background color is creamy white and there are a few rounded blotches of tan or light

brown spots between some of the tubercles. The tubercle stalks are white and the flattened tops are either all white or all tan. The rhinophores are creamy white on the specimens with white tubercle tops, or are yellowish on specimens with tan tubercle tops. The gill leaves are white.

Digestive system.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is rounded and the large radular sac protrudes noticeably from the posterior-ventral side (Fig. 44). There are two large pear-shaped oral glands that extend from the ventral side of the buccal bulb. The radular formula for a 5 mm specimen is 16 × 13.0.13 (Fig. 45). The jaw (Fig. 45A) is not well developed but has a thickened edge. The teeth are simply hamate, and the innermost tooth is much smaller and thinner than the remaining teeth. Rachidian teeth are absent. The outermost teeth are slightly larger than the middle lateral teeth.

Reproductive system.— The reproductive system is triaulic (Fig. 46). The ampulla is large and bulbous. It branches into the oviduct and the prostate. The prostate is long and tubular and coils twice, then narrows for a short distance before entering the wider deferent duct. The deferent duct enters the long penis, which is as wide as the deferent duct. The penis has small densely packed penial hooks at the distal tip only. The vagina is narrow and was not examined internally. Thus, the presence of spines or hooks cannot be confirmed. The short, narrow vaginal duct enters the bursa copulatrix at the proximal end. The receptaculum seminis connects to the bursa with a longer duct than the oviduct, which leads from the bursa into the female gland mass. The bursa is round and half the size of the ampulla. The receptaculum seminis is ovoid and is approximately one-half the size of the bursa.

Central nervous system.— The central nervous system has fused cerebral and pleural ganglia (Fig. 47). The eyes are mid-sized in comparison to other Aegiridae and are sessile on the cerebral-pleural complex. The pedal

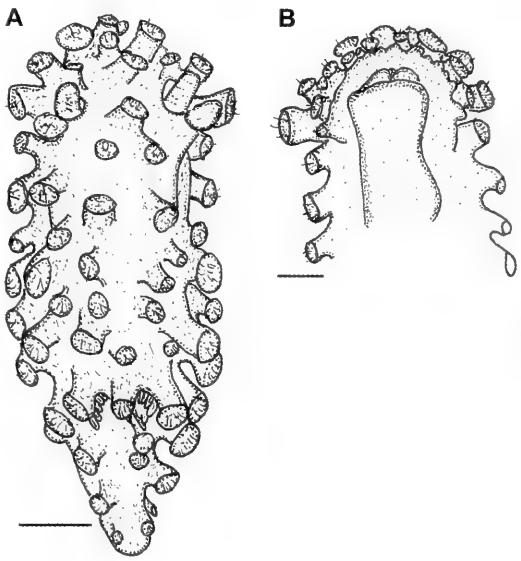


Figure 43. *Aegires incusus* sp. nov. CASIZ 070357. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.57 mm.

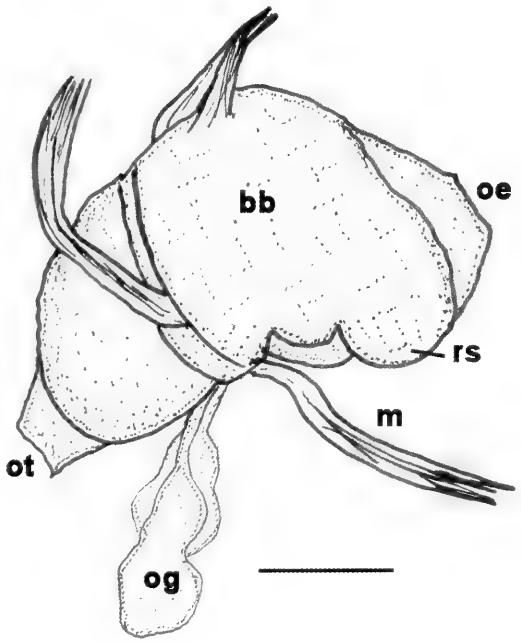


Figure 44. *Aegires incusus* sp. nov. CASIZ 156668. Buccal bulb: bb = buccal bulb, m = muscle, oe = esophagus, og = oral gland, ot = oral tube, rs = radular sac, scale = 0.25 mm.

ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

Circulatory system.— (not pictured) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— *Aegires incusus* is externally most similar to *Aegires pruvotfolae*. For a comparison between these two species, see the section under *Aegires pruvotfolae* in the present study. The particular combi-

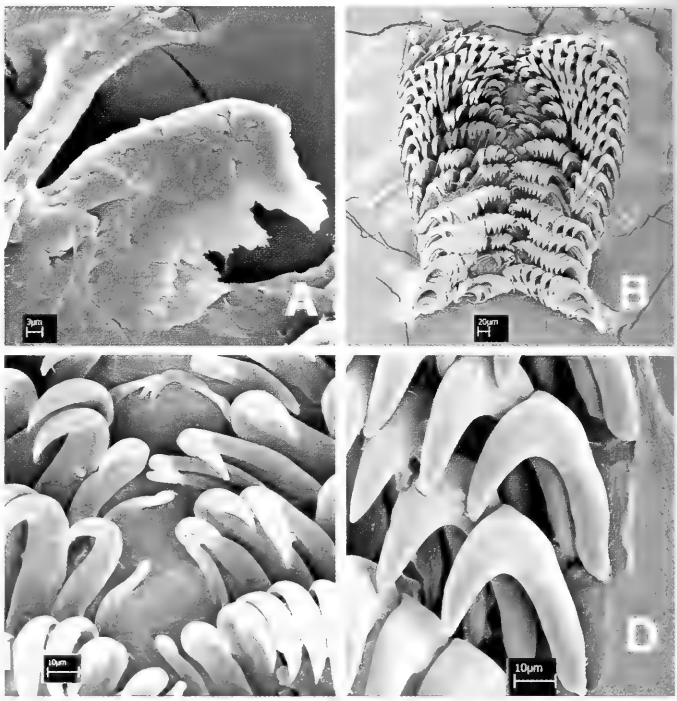


Figure 45. *Aegires incusus* sp. nov. CASIZ 156668. Buccal morphology: (A) Jaw, scale = 3 µm. (B) Whole radula, scale = 20 µm. (C) Inner lateral teeth, scale = 10 µm. (D) Outer lateral teeth, scale = 10 µm.

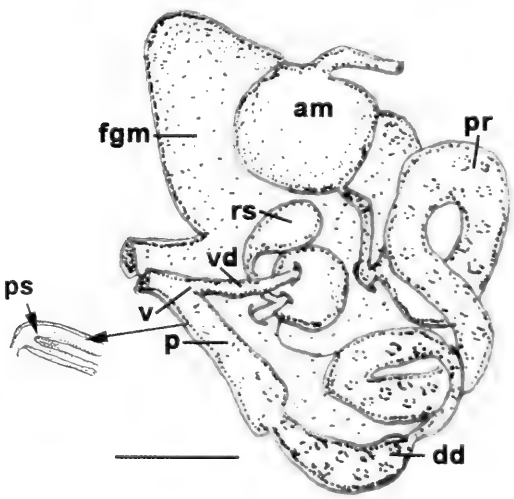


Figure 46. *Aegires incusus* sp. nov. CASIZ 156668. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, ps = penial spines, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.25 mm.

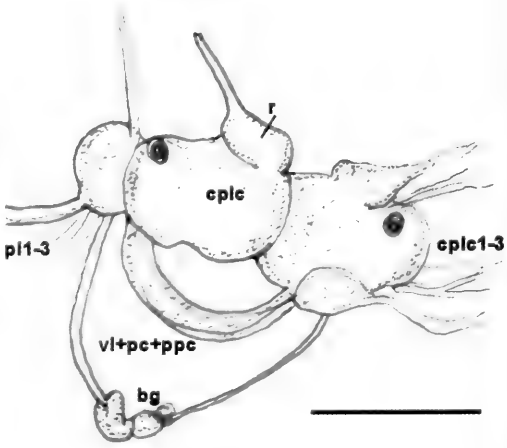


Figure 47. *Aegires incusus* sp. nov. CASIZ 086465. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.25 mm.

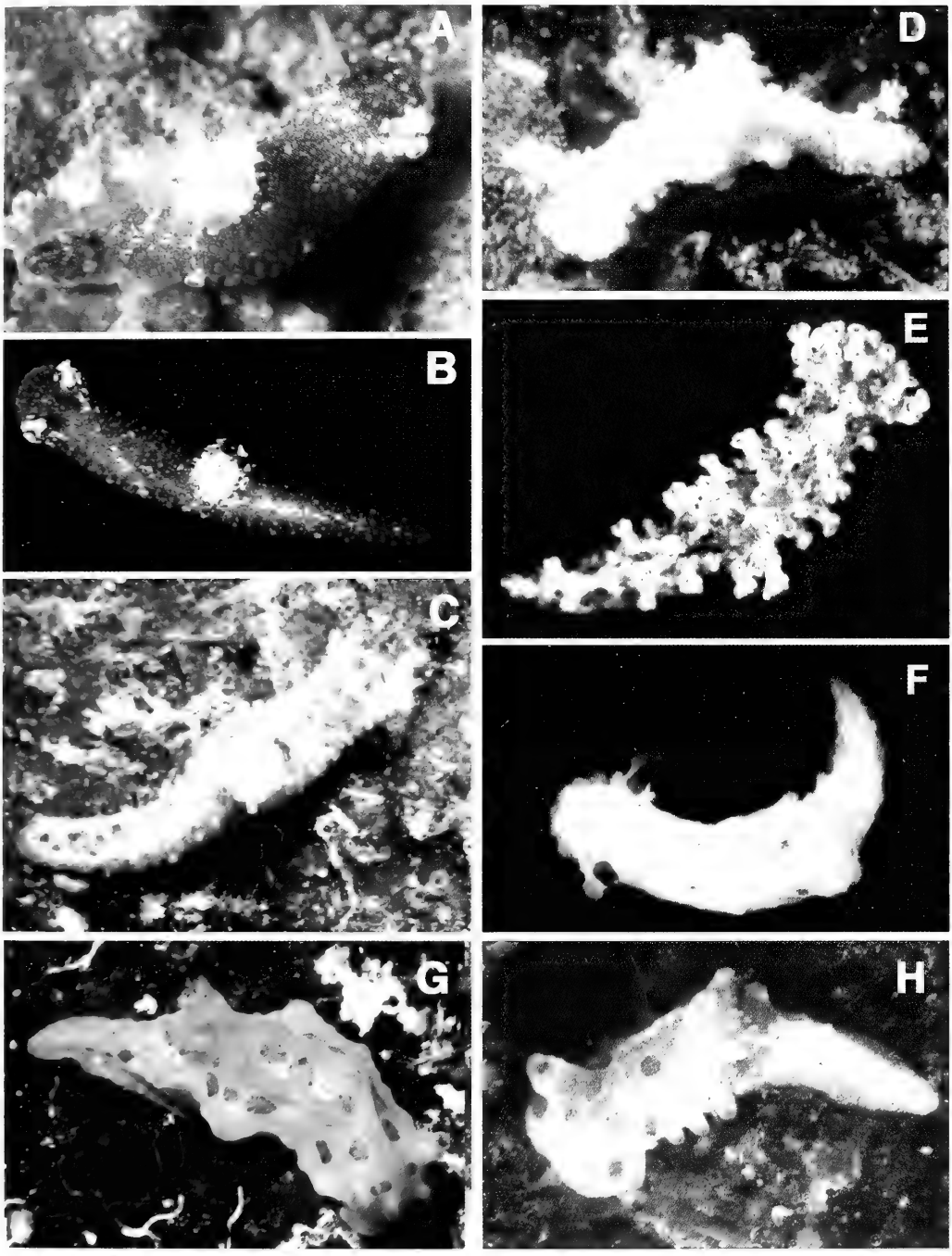


FIGURE 48. Photos of living specimens. (A) *Aegires flores* sp. nov. CASIZ 084277, photo by T. Gosliner, 5 mm. (B) *Aegires flores* sp. nov. CASIZ 078568, photo by P. Fiene, 9 mm. (C) *Aegires flores* sp. nov. CASIZ 120931, photo by S. Johnson, 12 mm. (D) *Aegires petalis* sp. nov. CASIZ 168920, photo by T. Gosliner, 5 mm. (E) *Aegires exeches*, CASIZ 078629, photo by P. Fiene, 4 mm. (F) *Aegires hapsis* sp. nov. CASIZ 115721, photo by R. Bolland, 6 mm. (G) *Aegires sublaevis*, CASIZ168923, photo by T. Gosliner, 12 mm. (H) *Aegires sublaevis* CASIZ, 078393, photo by T. Gosliner, 8 mm.

nation of external, reproductive and radular characters distinguish *A. incusus* as a distinct *Aegires* species.

Aegires flores Fahey and Gosliner, sp. nov.

(Figs. 48A–C, 49–53)

Aegires citrinus Nakano, 2004:117, no. 242, top and right photograph. Misidentification.
= *Aegires* sp. 3, Tanaka, 2001 in SeaSlug Forum.

Type material.— Holotype: CASIZ 120931, one specimen, 11 mm, Choptop Reef, Enewetak Atoll, Marshall Islands, 8 m, collected August 1988, S. Johnson. Paratypes: CASIZ 120930, one specimen, 13 mm, dissected, Bubble Butt Pinnacle, Enewetak Atoll, Marshall Islands, collected September 1983, S. Johnson. CASIZ 073059, one specimen, 9 mm, Pinnacle, Madang, Papua New Guinea, 5 m, collected, Oct, 1986, T. Gosliner. CASIZ 168922, Outer Reef, Bagabag Island, Papua New Guinea, collected July 1989, T. Gosliner. CASIZ 075909, one specimen, 4 mm, Barracuda Point, Pig Island, Papua New Guinea, 32 m, collected November 1990, T. Gosliner. CASIZ 075877, two specimens, 4 and 7 mm, dissected, Barracuda Point, Pig Island, Madang, Papua New Guinea, 34 m, collected November 1990, T. Gosliner. CASIZ 078568, one specimen, 9 mm, Bunaken Island, Manado, Sulawesi, 3 m, collected May 1991, P. Fiene. CASIZ 084277, one specimen, 5 mm, Devil's Point, Maricaban Island, Luzon, Philippines, 10 m, collected February 1992, T. Gosliner. CASIZ 157153, one specimen, 10 mm, Bethlehem, Maricaban Island, Luzon, Philippines, 7 m, collected May 2001, T. Gosliner.

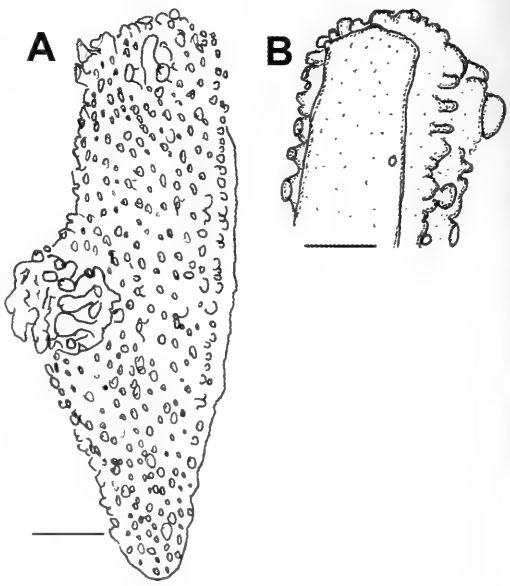


Figure 49. *Aegires flores* sp. nov. CASIZ 120930. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 1.3 mm.

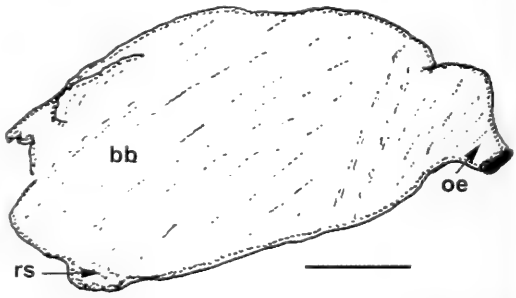


Figure 50. *Aegires flores* sp. nov. CASIZ 120930. Buccal bulb: bb = buccal bulb, rs = radular sac, oe = esophagus, scale = 0.25 mm.

Distribution.— This species has been reported from the Marshall Islands, Papua New Guinea, Sulawesi, the Philippine Islands (present study), and from Japan (Nakano and Tanaka 2004).

Etymology.— The specific name *flores* is from the Latin word meaning blossom, referring to the shape of the rhinophore and gill protective appendages of this species.

External morphology.— The body shape is elongate and slightly rounded (Figs. 48A–C, 49). The dorsum is completely covered by small raised tubercles, some with flat tops and some

with rounded tops. Spicules protrude from the tops of all tubercles. The rhinophore pocket is slightly elevated and is surrounded by approximately five flat-topped tubercles that vary in size. The tubercles on the exterior edge of the rhinophore pocket are large and rounded and look like flower petals. The rhinophores are smooth. The gill pocket lies mid dorsally and is surrounded by approximately twelve flattened, paddle-shaped tubercles in varying sizes, arranged like a crown or an opening flower. The small gill leaves are tripinnate.

The background color of the living animals is cream. The overlying colors range from gray-white with yellow-topped tubercles to brown with orange-topped tubercles. The paddle-shaped tubercles around the gill can be translucent white with white tips or translucent yellow with darker yellow tips. The rhinophores in all color forms are translucent white as are the gill leaves.

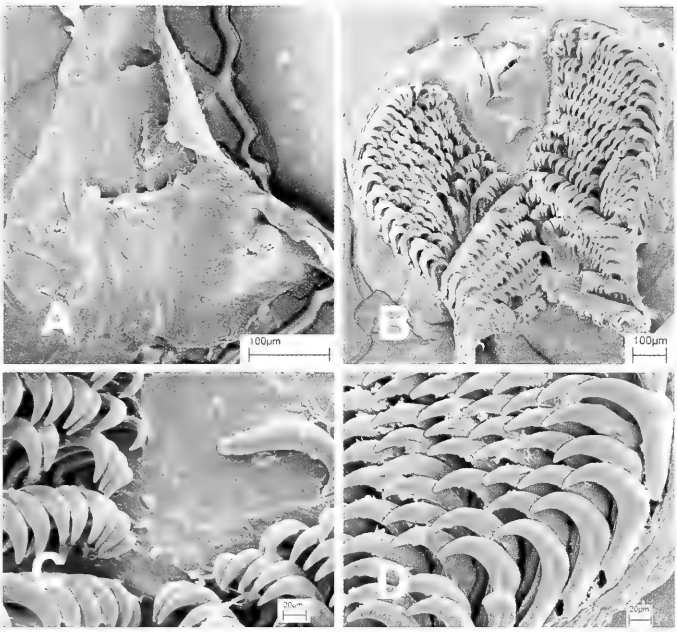


FIGURE 51. *Aegires flores*. sp. nov. CASIZ 120930. Buccal morphology: (A) Jaw, scale =100 µm. (B) Whole radula, scale = 100 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 20 µm.

DIGESTIVE SYSTEM.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes from the posterior side only very slightly (Fig. 50). The radular formula is 18 × 17.0.17 for a 7 mm

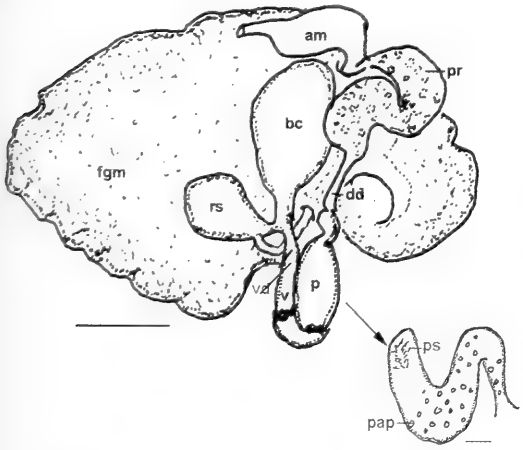


FIGURE 52. *Aegires flores* sp. nov. CASIZ 120930. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pap = papillae, ps = penial spines, pr = prostate, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.4 mm.

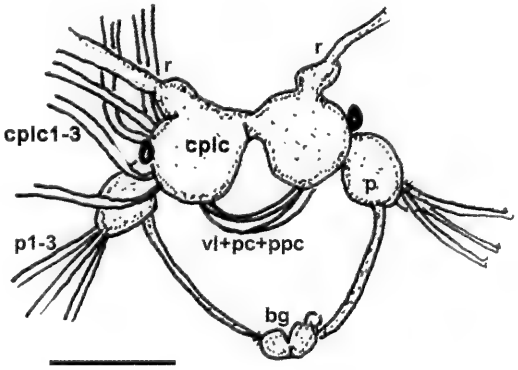


FIGURE 53. *Aegires flores* sp. nov. CASIZ 086465. Central nervous system: bg = buccal ganglia, cplc = cerebropleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.3 mm.

specimen (Fig. 51). The jaw (Fig. 51A) is not well developed but has a thickened edge. All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The oldest teeth have a longitudinal groove on the outer side, a slight bulge at the posterior midpoint and a longer hook than the remaining teeth.

Reproductive system.— The reproductive system is triaulic (Fig. 52). The ampulla is short and wide. It branches into the oviduct and the prostate. The prostate is relatively short, tubular and curves once before narrowing into the short deferent duct. The deferent duct then widens into the penis, which has small densely packed penial hooks at the distal tip. There are also several rows of papillae inside the penis, at the proximal end. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is long and narrow and at the proximal end, enters a common duct that connects the bursa copulatrix and the receptaculum seminis. The receptaculum is connected to the oviduct, which enters the female gland mass. The bursa is ovoid and much larger than the ampulla. The receptaculum is ovoid and is approximately one-third the size of the bursa.

Central nervous system.— The central nervous system has fused cerebral and pleural ganglia (Fig. 53). The eyes are small, sessile on the cerebral-pleural complex, but protrude slightly. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

Circulatory system.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— *Aegires flores* has a unique external morphology. Although it has an elongate body, a rounded posterior end of the foot, a tuberculate notum, protective tubercles around the rhinophores and gill, and smooth rhinophores, there are several unique characters that set this species apart. Most noticeably, the gill appendages have a unique paddle shape. The tubercles on the outside of the rhinophore pockets also resemble those around the gill, both in shape and in color. The dorsal tubercles are all much lower than the protective tubercles, a feature not shared by other *Aegires* species.

The reproductive morphology is also different from other *Aegires* species. The short, wide ampulla with a short deferent duct is a combination of characters not seen in other *Aegires* species. These features combined with the very short duct leading from the receptaculum to the bursa are not found in other *Aegires*.

The unusual combination of external and internal characters distinguishes *Aegires flores* as a new species.

Aegires petalis Fahey and Gosliner, sp. nov.

(Figs. 48D, 54–57)

Type material.— Holotype: CASIZ 168920, one specimen, 5 mm, dissected, Anemone Reef, Madang, Papua New Guinea, collected February 1988, T. Gosliner.

Distribution.— This species has only been reported from Papua New Guinea (present study).

Etymology.— The specific name *petalis* is taken from the Greek word *petalon* meaning a leaf or petal. This is in reference to the rhinophore sheaths of this new species.

External morphology.— The body shape is elongate and the dorsum is high (Fig. 48D).

Flat-topped raised tubercles are arranged in two lines along the anterior half of the dorsum. On the posterior half of the dorsum, the largest tubercles are arranged in a diamond pattern. Additional large, flat-topped tubercles line the edge of the dorsum. Long spicules protrude from the tops of all tubercles (Fig. 54). The rhinophore pocket is tall and cylindrical and has a petal-like outer edge. The rhinophores are smooth. The gill pocket lies mid dorsally and is protected by three appendages that have flattened tops. The small gill leaves are tripinnate.

The background color of the living animal is white, as are the tubercles, the rhinophores and the gill leaves. There are no additional colors on the specimen examined in this study.

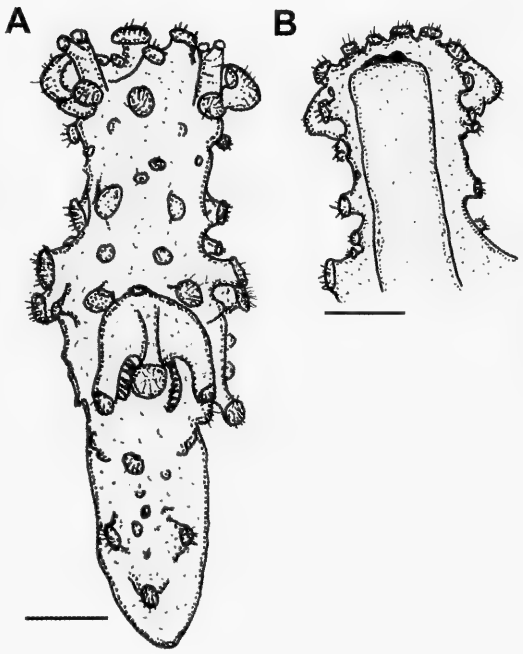


FIGURE 54. *Aegires petalis* sp. nov. CASIZ 168920. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.7 mm.

DIGESTIVE SYSTEM.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes from the posterior side only very slightly (Fig. 55). The radular formula is 13 × 13.0.13 for the 5 mm holotype (Fig. 56). The jaw (Fig. 56A) is not well developed but has a thickened edge. All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The three inner lateral teeth are thinner and smaller than the remaining teeth. The oldest teeth have a shallow longitudinal groove on the outer side.

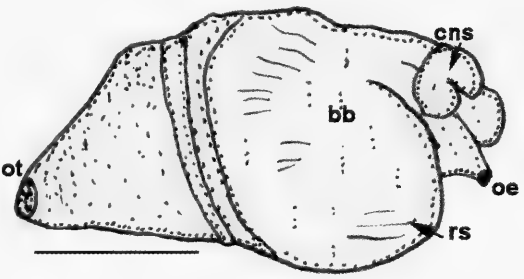


FIGURE 55. *Aegires petalis* sp. nov. CASIZ 168920. Buccal bulb: bb = buccal bulb, cns = central nervous system, oe = esophagus, ot = oral tube, rs = radular sac, scale = 0.3 mm.

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 57). The ampulla is elongate and narrow. It branches into the oviduct and the prostate. The prostate is long, tubular and coils once before narrowing into the long, thin deferent duct. The deferent duct then widens into the short but wide penis, which has small, densely packed hooks at the distal tip only. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is short and narrow and at the proximal end, enters the bursa copulatrix. A duct from the bursa enters the bifurcating oviduct that originates from the receptaculum. The oviduct enters the female gland mass. The bursa is ovoid and smaller than the round receptaculum.

CENTRAL NERVOUS SYSTEM.— The central nervous system has fused cerebral and pleural ganglia (not pictured). The eyes are small, sessile on the cerebral-pleural complex, and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two

buccal ganglia are positioned ventral to the esophagus.

Circulatory system.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Externally, *Aegires petalis* most closely resembles *A. ortizi*. Both species are either white or creamy yellow (*A. ortizi*) and have dorsal tubercles. However, the tubercles of *A. ortizi* are arranged in four longitudinal rows (Templado et al. 1987) whereas in *A. petalis* the tubercles are randomly scattered. *Aegires ortizi* also has brown coloration and minute white spots between the tubercles, which *A. petalis* does not have. There are three large tubercles on the outside of the rhinophore sheaths of *A. ortizi* but the rhinophore margins of *A. petalis* are elevated and multi-lobed. The three gill appendages of *A. petalis* have flattened tops, but in *A. ortizi* the appendages are pointed.

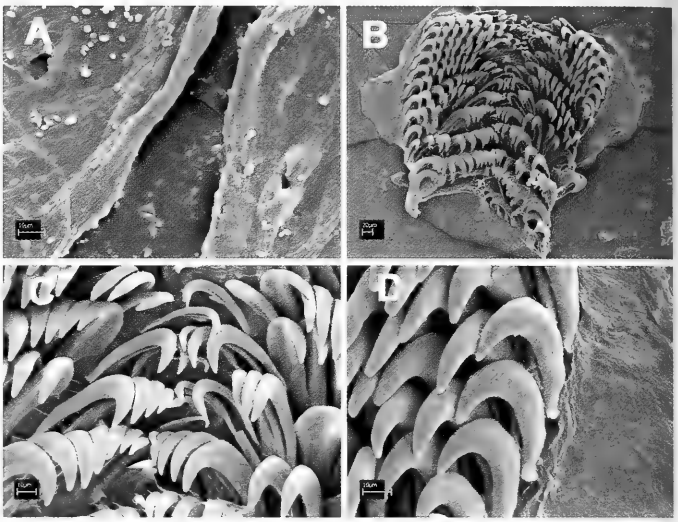


Figure 56. *Aegires petalis* sp. nov. CASIZ 168920. Buccal morphology: (A) Jaw, scale =10 μm. (B) Whole radula, scale = 20 μm. (C) Inner lateral teeth, scale = 10 μm. (D) Outer lateral teeth, scale = 10 μm.

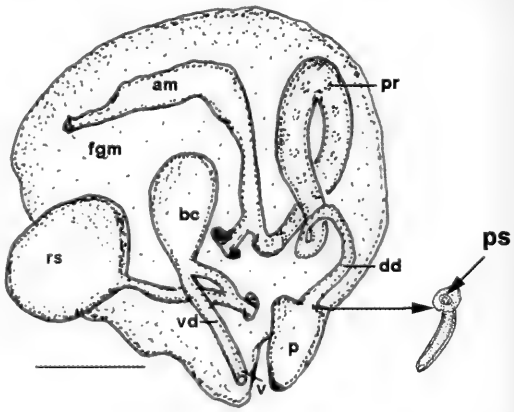


Figure 57. *Aegires petalis* sp. nov. CASIZ 168920. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis; pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina; vd = vaginal duct, scale = 0.5 mm.

The reproductive morphology differs between *Aegires petalis* and *A. ortizi*. Although both have an elongate ampulla, the ampulla of *A. petalis* is relatively longer. The penial morphology is noticeably different. The penis of *A. petalis* is short and thick, and that of *A. ortizi* is very long and wide. In addition, *A. petalis* only has penial spines at the distal tip while they are found throughout the penis of *A. ortizi*. The prostate of *A. ortizi* is also very thick and tubular, whereas in *A. petalis* it is much thinner and coiled. The receptaculum of *A. petalis* is larger than the bursa and connects to the common oviduct. But in *A. ortizi* the receptaculum is much smaller than the bursa and connects on a very long separate duct to the base of the bursa.

This combination of morphological characters sets *A. petalis* apart from other species of *Aegires*.

***Aegires exeches* Fahey and Gosliner, sp. nov.**
(Figs. 48E, 58–61)

Aegires punctilucens Nakano, 2004:117, no. 243. Misidentification.

Aegires punctilucens Imamoto 2002: photos, SeaSlug Forum. Misidentification.
Aegires punctilucens Ono, 1999:71, no. 103. Misidentification.
Aegires cf. *punctilucens* Marshall and Willan, 1999:59, pl. 93. Misidentification.
Aegires punctilucens Baba, 1974:11-12, Fig. 1. Misidentification.

Type material.— Holotype: CASIZ 078629, 4 mm, Hekili Point, Maui, Hawaii, 1 m, collected May 1991, C. Pittman. Paratype: CASIZ 168918, 4 mm, dissected, Hekili Point, Maui, Hawaii, 1 m, collected May 1991, C. Pittman. Paratypes: CASIZ 109790, 3 mm, Pig Island, Madang, Papua New Guinea, no depth available, collected October 1996, T. Gosliner. CASIZ 068750, 2 mm, Jais Aben, Madang, Papua New Guinea, 15 m, collected July 1989, T. Gosliner. CASIZ 075804, 2 mm, between Wongat and Tabat Islands, Madang, Papua New Guinea, 23 m, collected November 1990, T. Gosliner, G. Williams, M. Jebb. CASIZ 079183, 2 mm, Horseshoe Cliffs, Onna Village, Okinawa, 5 m, collected June 1991, T. Gosliner. CASIZ 115394, 4 mm, Maeki-zaki, Seragaki, Okinawa, 46 m, collected, April 1997, R. Bolland.

Distribution.— This species has been reported from Hawaii, Japan, Papua New Guinea (present study), the Marshall Islands (S. Johnson photo) and the Great Barrier Reef, Australia (Marshall and Willan 1999).

Etymology.— The specific name *exeches* is from the Greek *exechos* meaning jutting out, projecting, prominent, which refers to the shape of the tubercles on this species.

External morphology.— The body shape is elongate and the posterior end of the foot ends in a point (Fig. 48E). There are numerous compound tubercles projecting from the dorsum, such that the body appears to be composed completely of tubercles (Fig. 58). The tubercles are elongate and narrow slightly before mushrooming into a flattened plate-like top. From the flattened tops, multiple spicules protrude. The rhinophore pockets are very long and are composed of two main tubercles on the anterior side, two shorter tubercles on the posterior side and much smaller tubercles in between. The rhinophores are smooth and have bifid apices. The gill protective appendages are also composed of elaborate tubercles. The gill leaves themselves are small, inconspicuous and tripinnate.

Figure 58. *Aegires exeches* sp. nov. CASIZ 168918. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.7 mm.

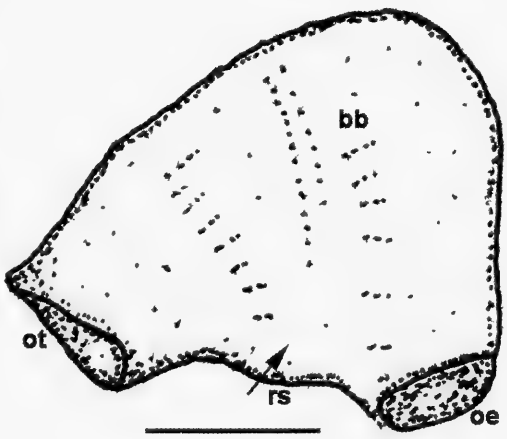


Figure 59. *Aegires exeches* sp. nov. CASIZ 168918. Buccal bulb: bb = buccal bulb, oe = esophagus, ot = oral tube, rs = radular sac, scale = 0.17 mm.

The background color ranges from white to tannish-white. The tops of the tubercles on the tan specimens have dark spots. The specimen from Enewetak, Marshall Islands is completely white. It has three evenly spaced, pale tan rings around the rhinophores. The tan specimens have three to four blue spots on the dorsum. These spots are arranged symmetrically, with two just posterior to the rhinophores, one at the centerline in front of the gill and the fourth at centerline just posterior to the gill.

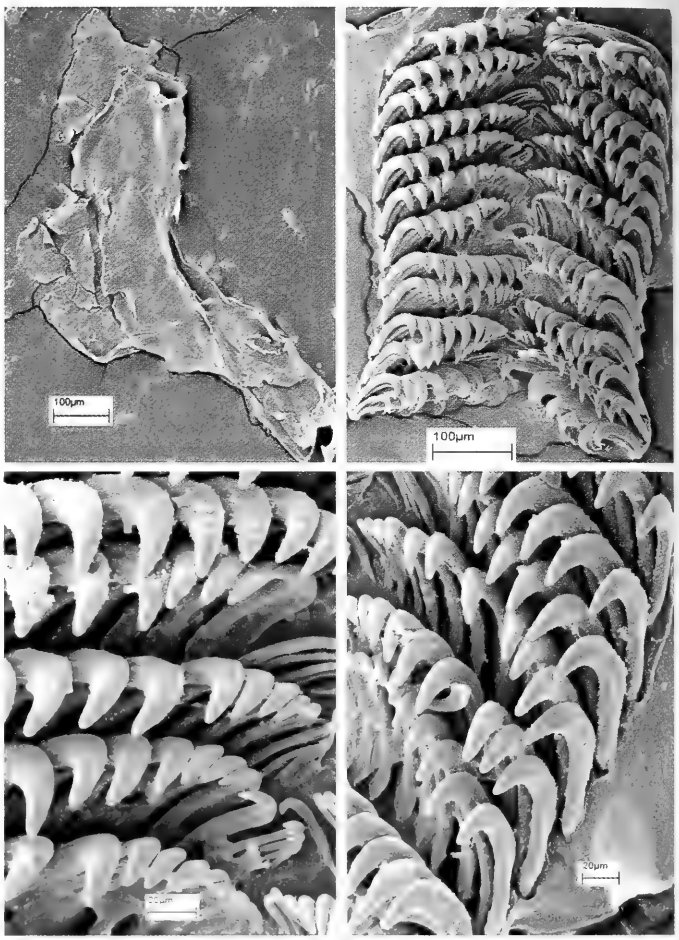


FIGURE 60. *Aegires exeches* sp. nov. CASIZ 168918. Buccal morphology: (A) Jaw. Scale =100 µm. (B) Whole radula. Scale = 100 µm. (C) Inner lateral teeth. Scale = 20 µm. (D) Outer lateral teeth. Scale = 20 µm.

DIGESTIVE SYSTEM— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes from the posterior side only very slightly (Fig. 59). The radular formula is 13 × 11.0.11 for the 4 mm specimen (Fig. 60). The jaw is not well developed but has a thickened edge (Fig. 60A). All teeth are simply hamate, with a short hook. Rachidian teeth are absent. The three inner lateral teeth are thinner and smaller than the remaining teeth. The oldest teeth have a shallow longitudinal groove on the outer side.

REPRODUCTIVE SYSTEM.— The reproductive system is triaulic (Fig. 61). The ampulla is a very long, thick tube. It branches into the oviduct and the prostate. The prostate is shorter, but also tubular and does not coil before narrowing into the very long, thin deferent duct. The deferent duct coils once near the entry to the wide penis, which has small irregularly spaced hooks along the entire length of the penis. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is long and narrow and at the proximal end, enters the bursa copulatrix. The bifurcating oviduct, which originates from the small ovoid receptaculum seminis, enters the vaginal duct. The oviduct enters the female gland mass. The bursa is small and nearly round.

CENTRAL NERVOUS SYSTEM.— The central nervous system has fused cerebral and pleural ganglia (not pictured). The eyes are small, sessile on the cerebral-pleural complex, and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the

visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebropleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

Circulatory system.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Externally, *Aegires exeches* most closely resembles *A. punctilucens* from the Mediterranean. However, there are both external and internal differences that separate these two species. The most obvious external differences are the body shape, rhinophoral apices, gill protective structure morphology and tubercle arrangement. *Aegires exeches* has a very elongate body with extremely elevated, unique tubercles. That is, they are nearly mushroom-shaped, with a flat crown and completely cover the dorsum. D'Orbigny also described the body shape of *A. punctilucens* as being elongate, with a broadening at the midpoint. He described the tubercles of *A. punctilucens* as conical, with a flattened top, and a definite symmetry to their arrangement. Schmekel and Portmann (1982) also illustrated and described the tubercles on the specimens from the Mediterranean as being much shorter and wider at the base and symmetrically arranged, such that there are smooth parts of the dorsum visible between them. In *A. exeches*, no smooth spaces exist between the tubercles, which are taller, narrower at the base and more densely arranged than on *A. punctilucens*.

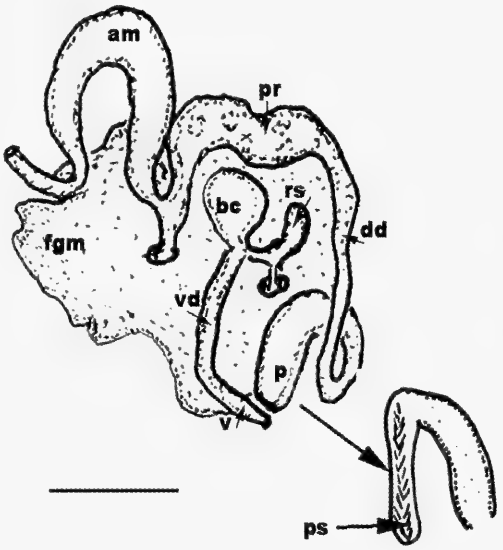


Figure 61. *Aegires exeches* sp. nov. CASIZ 168918. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

The rhinophores of *A. exeches* have bifid apices whereas the rhinophores of *A. punctilucens* do not (see Schmekel and Portmann 1982 for an illustration).

The gill protective structure of *Aegires exeches* is also different from that of *A. punctilucens*. *Aegires exeches* has a very elaborate, lobed gill structure, while *A. punctilucens* has three simple tubercles (see Schmekel and Portmann 1982 for a drawing of the Mediterranean specimens).

When comparing the external coloration, both species can be white or light brown. But Schmekel and Portmann describe minute opaque white dots spotted over the brown color, and the iridescent "eye" spots have a brownish-red circular area around them, bordered with black-brown dots. Specimens of *Aegires exeches* from Okinawa, Hawaii and the Marshall Islands do not have any opaque white dots over the dorsal color, but do have iridescent spots, although in much fewer numbers than is found on *A. punctilucens*. The "eye" spots on *A. exeches* can also be surrounded by a border of black-brown dots and a smooth orange circle surrounding the center as seen in photos on the SeaSlug Forum (Rudman 2004).

There are significant differences in the reproductive morphology between these two species. Although d'Orbigny didn't describe or illustrate the reproductive organs of *A. punctilucens*, Schmekel and Portmann drew the anatomy of specimens from the Mediterranean. Most noticeably, *A. exeches* has a receptaculum seminis that attaches to the base of the bursa copulatrix. In *A. punc-*

tilucens the receptaculum connects directly to the bulbous vagina. The prostate of *A. exeches* is short, tubular and nearly as thick as the ampulla, whereas in *A. punctilucens* the prostate is very thick and sausage-shaped and very coiled. *Aegires exeches* has a very long, tubular ampulla, a narrow vagina and a long, thin vaginal duct. *Aegires punctilucens* has a very bulbous ampulla and a very wide vagina, with a thick vaginal duct.

There are two differences in the radular teeth between these two species. Schmekel and Portmann illustrate an inner lateral tooth that is substantially smaller than the rest of the teeth in the row. They also state that the size increases outwards. In *A. exeches*, the first three lateral teeth are smaller than the remaining teeth, which are all the same size. In *A. exeches,* the radular formula is 14 × 11.0.11 for a 4 mm specimen. Schmekel and Portmann give a radular formula for a 6 mm specimen of 16 × 18.0.18.

Baba (1974) described a specimen found in the Sado district of the Japan Sea as *Aegires punctilucens*. Comparison of Baba's drawings and description of that specimen to our specimens of *Aegires exeches* leads us to believe that Baba's specimen is also *A. exeches.*

Whereas *A. exeches* bears some external similarities to the Mediterranean *A. punctilucens*, the Indo-Pacific specimens clearly represent a distinct species.

Aegires hapsis Fahey and Gosliner, sp. nov.

(Figs. 48F, 62–66)

Type material.— Holotype: CASIZ 115721, one specimen, 6 mm, dissected, Horseshoe Cliffs, Okinawa, Ryukyu Islands, 3 m, collected March 1998, R. Bolland.

Distribution.— This species has only been reported from Okinawa (present study).

Etymology.— The specific name *hapsis* is a Greek word meaning mesh or network, a word that describes the fine white webbing that covers the dorsum of this species.

External morphology.— The body shape is elongate (Fig. 48F, 62). The dorsum has small raised tubercles, arranged in a somewhat regular fashion on the sides of the dorsum and along the midline behind the gill. Spicules protrude from the tops of all tubercles. The rhinophore pocket is raised and the outer edge is formed by three large tubercles. The rhinophores are smooth. The gill pocket lies in the posterior third of the dorsum and is protected by a tri-lobed appendage. Each appendage is further divided into 4–5 smaller lobes. The small gill leaves are tri-pinnate.

The background color is pale tan and white. There is a fine network of white webbing covering the dorsum, especially noticeable on the posterior third, behind the gill pocket. There are small brown dots on either side of the dorsum midline. The tubercles that lie on the edge of the rhinophore pocket have a dark brown top. The rhinophores are dark brown. The gill branches are white.

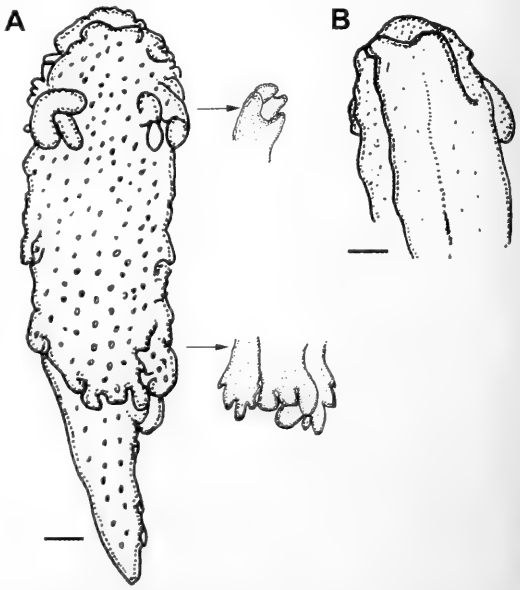


Figure 62. *Aegires hapsis* sp. nov. CASIZ 115721. Drawing of preserved animal. (A) Dorsal view. (B) Ventral view of head. Scale = 0.4 mm.

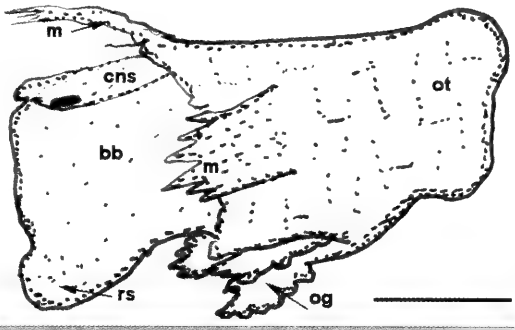


FIGURE 63 (right). *Aegires hapsis* sp. nov. CASIZ 115721. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscle, oe = esophagus, og = oral glands, ot = oral tube, rs = radular sac, scale = 0.3 mm.

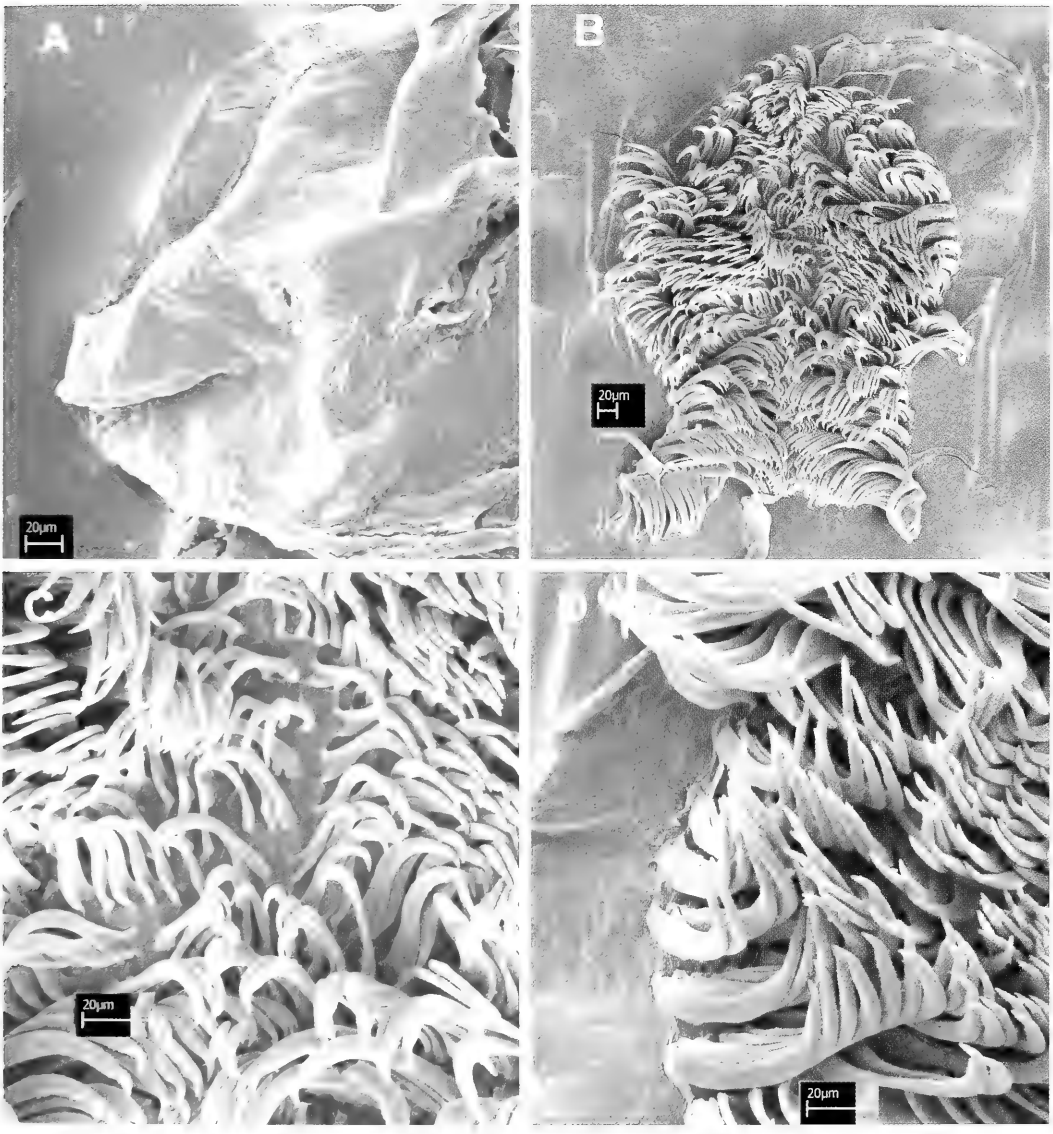


FIGURE 64. *Aegires hapsis* sp. nov. CASIZ 115721. Buccal morphology: (A) Jaw, scale =20 µm. (B) Whole radula, scale = 20 µm. (C) Inner lateral teeth, scale = 20 µm. (D) Outer lateral teeth, scale = 20 µm.

Digestive system.— The arrangement of the digestive system is as illustrated for other *Aegires* (see Figs. 3B, 8B). The buccal bulb is more ovoid than round and the radular sac protrudes noticeably from the posterior side (Fig. 63). Large oral glands on either side of the oral tube extend markedly from the base of the oral tube. The radular formula is difficult to confirm owing to the very compressed, flattened tooth arrangement, but is approximately 18-20 × 20-21.0.20-21 for the 4 mm specimen (Fig. 64). The jaw (Fig. 64A) has a thickened edge and rounded thickenings at each side. All teeth are hamate, with a long hook on the inner lateral teeth and a shorter hook on the outer teeth. The tips of the teeth are recurved. Rachidian teeth are absent. Some inner lateral teeth have a sharper hook than the remaining teeth. There is no longitudinal groove on the oldest lateral teeth as found in other *Aegires* species.

Reproductive system.— The reproductive system is triaulic (Fig. 65). The ampulla is very large and bulbous. It branches into the oviduct and the prostate. The prostate is tubular and coils once before narrowing into the very long, thin deferent duct. The deferent duct then widens into the penis. The penis was subsequently lost during preparation, and thus the presence of hooks could not be confirmed. The vagina is narrow and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is long and narrow and at the proximal end, enters the bursa copulatrix. The bifurcating oviduct, which originates from the small peanut-shaped receptaculum seminis, enters the vaginal duct. The oviduct enters the female gland mass. The bursa is ovoid and small.

Central nervous system.— The central nervous system has fused cerebral and pleural ganglia (Fig. 66). The eyes are small, sessile on the cerebral-pleural complex, and do not protrude. The pedal ganglia are slightly smaller than the cerebral-pleural complex and they are joined by the visceral loop-pedal/parapedal commissures. Three prominent nerves lead from the pedal ganglia and four nerves, including the rhinophoral nerve, originate from the cerebro-pleural ganglia. Two buccal ganglia are positioned ventral to the esophagus.

Circulatory system.— (not shown) As with other species of *Aegires*, the heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Externally, *Aegires hapsis* does not closely resemble any other *Aegires* species. Only *A. malinus* has a similarly smooth dorsum with a fine network pattern overall and tiny dorsal

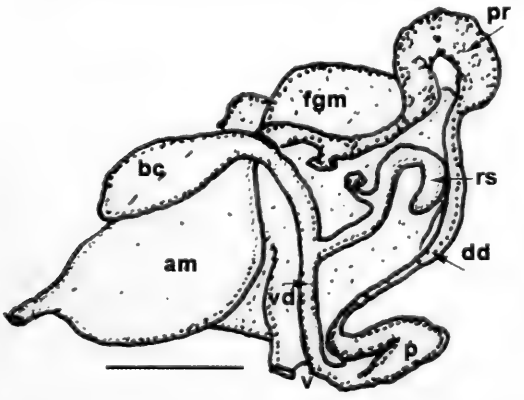


Figure 65. *Aegires hapsis* sp. nov. CASIZ 115721. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, r = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.25 mm.

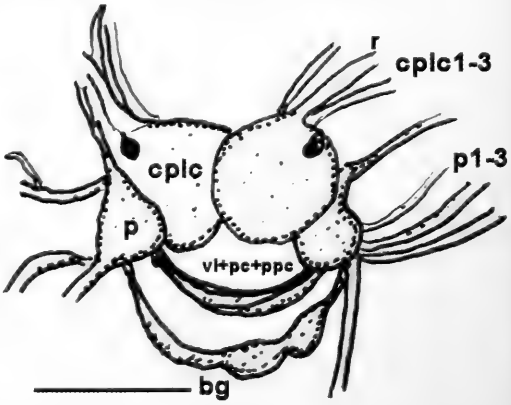


Figure 66. *Aegires hapsis* sp. nov. CASIZ 115721. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.25 mm.

tubercles. But that species has a very different background color (red-brown) and apple green rhinophoral and gill appendages.

The radular teeth of *A. hapsis* are different from other species as well. In *A. hapsis* the teeth are much more elongate and numerous than found in other species. For example, the inner lateral teeth have a longer hook than the outer lateral teeth and most teeth have a downward bend at the tip. This feature is not found in any other *Aegires* species.

The reproductive morphology has some similarities to other *Aegires*. The long thin deferent duct and the wider, tubular prostate are features shared with *A. execches, A. incusus* and *A. malinus*. *Aegires ninguis* and *A. incusus* also have a large, balloon-shaped ampulla like *A. hapsis*. However, the combination of a large ampulla, a long thin deferent duct with a wider prostate combined with a receptaculum that leads from a separate duct into the vaginal duct is not shared by any of the other *Aegires* species.

The particular combination of morphological characters separates *Aegires hapsis* as a distinct species.

Taxa formerly included in the Genus *Notodoris* Bergh, 1875

TYPE SPECIES: *Notodoris citrina* Bergh, 1875:64, by monotypy.

DIAGNOSIS.— Both Bergh (1875) and Eliot (1906) provided a complete diagnosis for the genus: the body is limaciform, with no distinction between the back and sides. The body is hard, rough and rugose and the surface is filled with spicules. The frontal veil is large. The rhinophores are smooth, retractable and protected by valves. The gill is protected by a large valve, is sometimes quite ramified and not retractable. The radula has no rachidian tooth, but has numerous hamate uniform lateral teeth, which have a rudimentary secondary denticle below the main hook.

REMARKS.— Bergh did not assign the family name Notodorididae to his new genus. The first author to use this name was Eliot (1910). See the earlier discussion on the history of the classification.

Aegires citrinus (Bergh, 1875)

(Figs. 67–71)

Notodoris citrina Bergh, 1875:53–100
Aegires citrinus (Bergh) comb. nov.

TYPE MATERIAL.— Rarotonga, Pacific Ocean. The type material has been lost and therefore, specimens from other Indo-Pacific localities have been examined for this study.

MATERIAL EXAMINED.— CASIZ 116864, one specimen, 52 mm, dissected. Rottnest Island, Western Australia, collected December 1998, S. Fahey. CASIZ 113597, one specimen, 23 mm, dissected. Laiwan Island, Louisiade Archipelago, Papua New Guinea, collected June 1998, T. Gosliner.

DISTRIBUTION.— Australia, Cook Islands, Fiji, Marshall Islands, Papua New Guinea, Solomon Islands, and New Caledonia (Bergh 1875; SeaSlug Forum, accessed 1 March 2004 and present study).

EXTERNAL MORPHOLOGY.— Bergh (1878) described the external morphology of this species. No differences were found between Bergh's description and the specimens examined for the present study.

DIGESTIVE SYSTEM.— *Aegires citrinus* shares the same general digestive anatomy (Fig. 67) as other *Aegires* (formerly *Notodoris*) species (Figs. 3B, 8B). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the diges-

tive gland. The buccal bulb is nearly round, with four large muscles attached, two per side (Fig. 67). The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick plate at the top of the opening, with no indication of rods at the edge (Figs. 68A, 69A). The radular teeth of the specimens examined from Western Australia and the Marshall Islands are as described by O'Donoghue (1924). That is, the teeth are so closely packed together that they are difficult to count (Figs. 68–69). The teeth are tall and hamate, with a small denticle under the tip of each tooth. All lateral teeth are similar in size and there is no sign of a rachidian tooth.

Reproductive system.— The reproductive system is triaulic (Fig. 70). The ampulla is very long, thick and tubular. It branches into the oviduct and the prostate. The tubular prostate is thinner, though much longer and coiled than the ampulla and it narrows appreciably into the short deferent duct. The deferent duct enters the very wide penis. The penis has small, sparsely spaced penial hooks near the opening at the genital atrium. The vagina is much narrower than the penis. It was not examined internally and thus the presence of spines or hooks cannot be confirmed. At the proximal end, the long, narrow vaginal duct enters the bursa copulatrix. The receptaculum seminis connects to the bursa via a long separate duct that bifurcates into the oviduct, which enters the female gland mass. The bursa is round and the same size as the large, ovoid receptaculum seminis.

Central nervous system.— As with species of both *Notodoris* and *Aegires*, the cerebral and pleural ganglia are fused together (Fig. 71). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

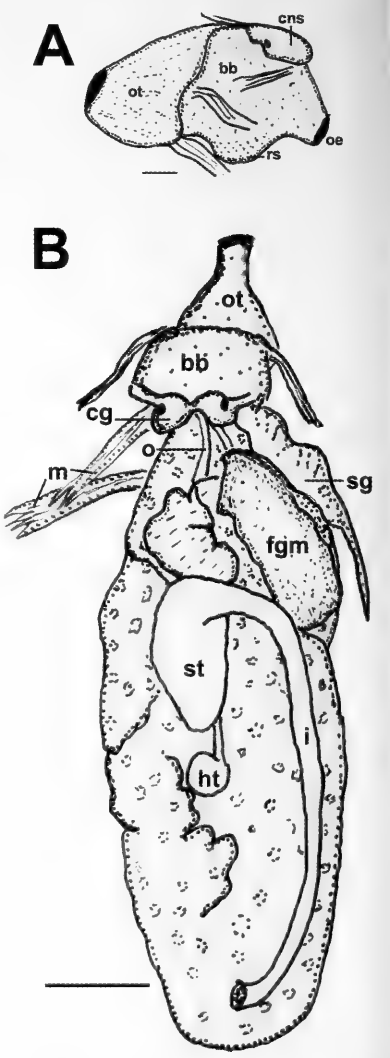


FIGURE 67. *Aegires citrinus* (Bergh, 1875). (A) Buccal bulb: CASIZ 113597. Scale = 0.46 mm. bb = buccal bulb, cns = central nervous system, oe = esophagus, ot = oral tube, rs = radular sac. (B) Digestive system: CASIZ 116864. Scale = 6.4 mm. bb = buccal bulb, cg = cerebral ganglia, fgm = female gland mass, ht = heart, i = intestine, m = muscles, o = esophagus, ot = oral tube, st = stomach, sg = salivary glands.

Circulatory system.— The heart (Fig. 67B) is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Bergh's (1875) description of this species was thorough and his drawings

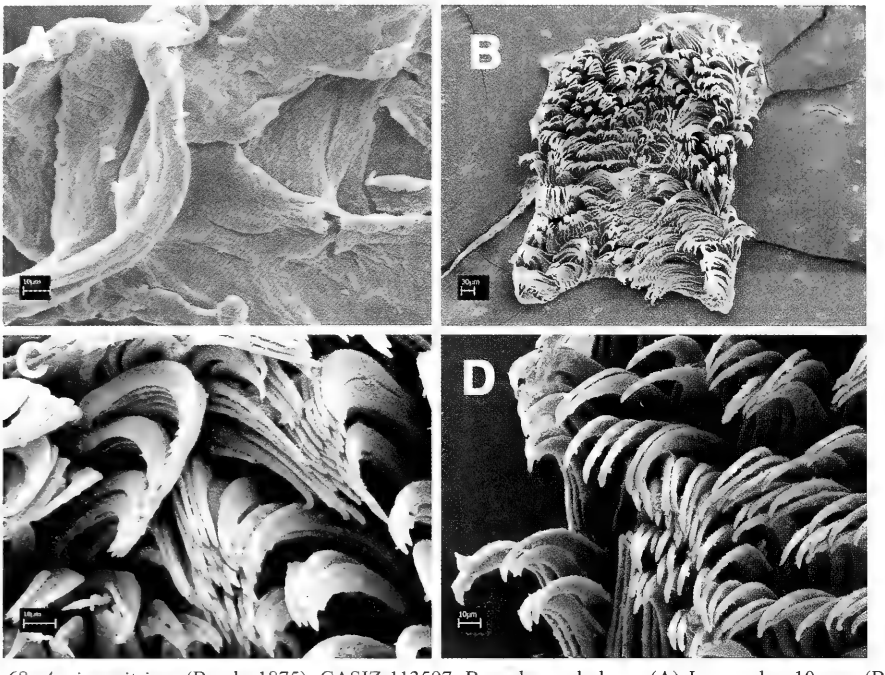


FIGURE 68. *Aegires citrinus* (Bergh, 1875). CASIZ 113597. Buccal morphology: (A) Jaw, scale =10 μm. (B) Whole radula, scale = 30 μm. (C) Inner lateral teeth, scale = 10 μm. (D) Outer lateral teeth, scale = 10 μm.

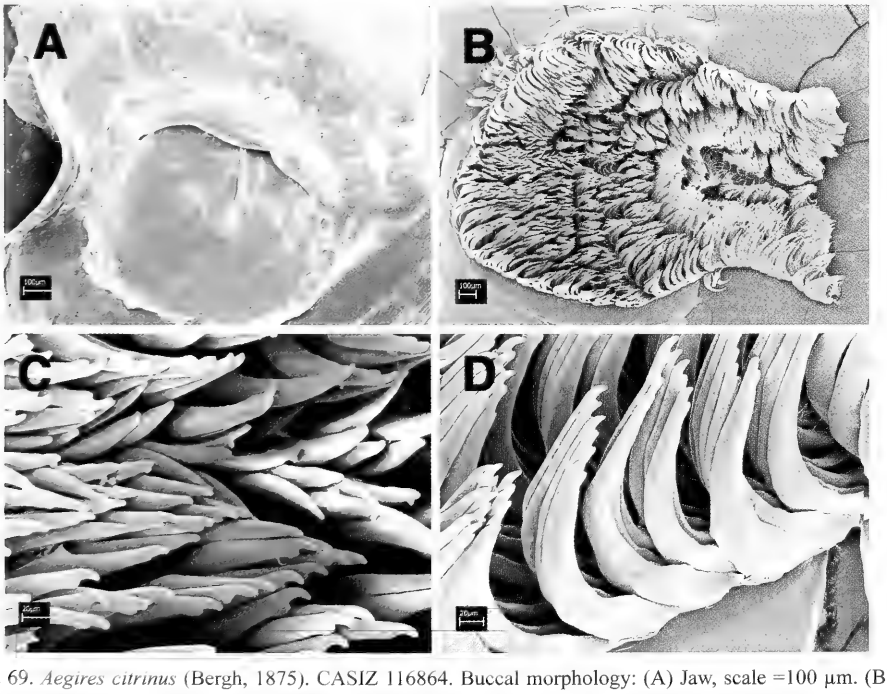


FIGURE 69. *Aegires citrinus* (Bergh, 1875). CASIZ 116864. Buccal morphology: (A) Jaw, scale =100 μm. (B) Whole radula, scale = 100 μm. (C) Inner lateral teeth, scale = 20 μm. (D) Outer lateral teeth, scale = 20 μm.

FIGURE 70 (right). *Aegires citrinus* (Bergh, 1875). CASIZ 116864. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 1.4 mm.

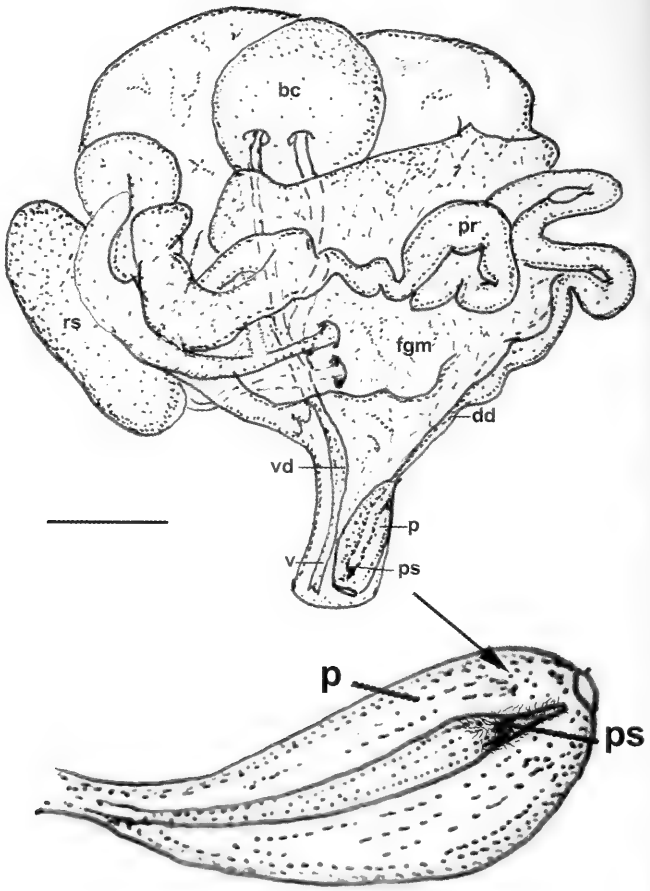
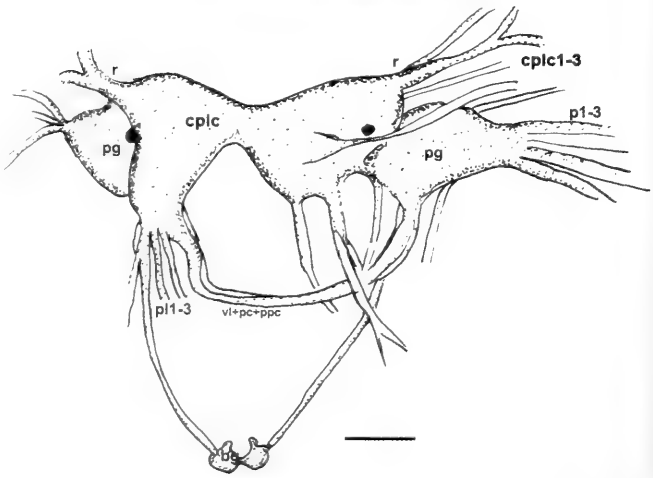


FIGURE 71. *Aegires citrinus* (Bergh, 1875). CASIZ 116864. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, pg = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.5 mm.



include the external, radular, reproductive and central nervous system morphology. O'Donoghue (1924) provided additional details of the anatomy and radular morphology and Gosliner and Behrens (1997) examined all *Notodoris* species except *N. citrinus* during their study of the new species, *N. serenae*. However, none of these recent authors confirmed Bergh's descriptions of the central nervous system, reproductive or digestive systems of *Notodoris citrinus*. For the present study, specimens were examined from localities other than the type locality to determine the extent of variation.

Aegires gardineri (Eliot, 1906)

(Fig. 72)

Notodoris gardineri Eliot, 1906: 540–573, pl. 32.
Notodoris megastigmata Allan, 1932:103.
Aegires gardineri (Eliot) comb. nov.

Type material.— Hulule, Maldive Islands. Holotype: 1919.10.7.47, one specimen, 3.35 cm, collected by Professor J.S. Gardiner, British Museum of Natural History.

Material examined.— CASIZ 106060, one specimen, 50 mm, dissected. Okinawa, Ryukyu Islands, collected 14 May 1995, R. Bolland.

Distribution.— Maldive Islands, Indonesia, Papua New Guinea, Okinawa, Western Caroline Islands, Solomon Islands and Australia (Eliot 1906; Marshall and Willan 1999; Coleman 2001; Rudman 2004; present study).

External morphology.— The external morphology of *Notodoris gardineri* was described in detail by several authors (O'Donoghue 1924; Yonow 1993; Rudman 2004).

Reproductive system.— Gosliner and Behrens (1997) illustrated and described the reproductive anatomy of *Notodoris gardineri*.

Digestive system.— *Aegires* (formerly *Notodoris*) *gardineri* shares the same general digestive anatomy as other *Notodoris* species (Fig. 67B). The buccal bulb is nearly round, with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thin cuticle (see also O'Donoghue 1924 and Yonow 1993). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

Central nervous system.— As with other species of previously included *Notodoris*, the cerebral and pleural ganglia are fused together (Fig. 72). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-

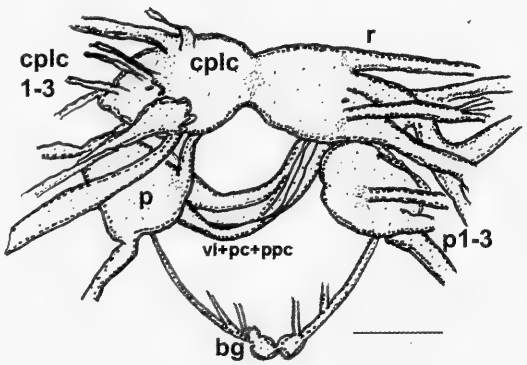


Figure 72. *Aegires gardineri* (Eliot, 1906). CASIZ 106060. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.5 mm.

esophageal, rhinophoral and optical ganglia are present.

Circulatory system.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Eliot (1906) described both the external and radular morphology of *Notodoris gardineri.* However, he did not describe nor illustrate the radular teeth except to note that they fit Bergh's (1875) plate IX exactly. O'Donoghue (1924) and Yonow (1993) provided further descriptions of the radular morphology.

Eliot also did not examine the reproductive anatomy, stating that the specimen he obtained was "too hardened" to examine. Although Gosliner and Behrens (1997) examined all *Notodoris* species except *N. citrinus*, they did not describe the central nervous systems or the digestive systems of the previously included *Notodoris* species. Therefore, additional specimens were examined to complete the data for the present study.

Aegires minor (Eliot, 1904)

(Figs. 73–74)

Notodoris minor Eliot, 1904: 83–105, pls 3–4.
Aegires minor (Eliot) comb. nov.

Type material.— Chuaka, East coast of Zanzibar. Type: 1919.9.16.4, one specimen, 13 mm. British Museum of Natural History.

Material examined.— CASIZ 068668, fourteen specimens; one specimen, 65 mm dissected. Madang, Papua New Guinea, collected August 1989, T. Gosliner.

Distribution. Zanzibar, Mauritius, Oman, Philippines, Eastern Caroline Islands, Solomon Islands, Papua New Guinea, Manado, Sulawsi, Indonesia, and Australia (Eliot 1904; Gosliner, Behrens, and Williams 1996; Rudman 2004).

External morphology.— The external morphology of the specimens examined for this study is as described by Eliot (1904) and corroborated by O'Donoghue (1924), Yonow (1993) and Gosliner and Behrens (1997).

Digestive system.— *Aegires minor* shares the same general digestive anatomy as other *Notodoris* species (Fig. 67B). The buccal bulb is nearly round (Fig. 73) with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a cuticle. The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

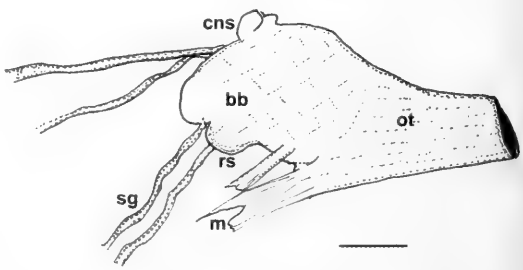


Figure 73. *Aegires minor* (Eliot, 1904). CASIZ 068668. Buccal bulb: bb = buccal bulb, cns = central nervous system, m = muscles, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 1.75 mm.

Central nervous system.— As with other species of *Aegires* (formerly *Notodoris*), the cerebral and pleural ganglia are fused together (Fig. 74). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to

most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

Circulatory system.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— Eliot (1904) described the external and the radular morphology of this species, but only described and drew one feature of the reproductive anatomy: the armed penis. Gosliner and Behrens (1997) examined all *Notodoris* species during their study of the new species *N. serenae*. But they did not describe the central nervous systems or the digestive systems of *Aegires* (*Notodoris*) at that time. Therefore, additional specimens of *Aegires minor* were examined to complete the data for the present study.

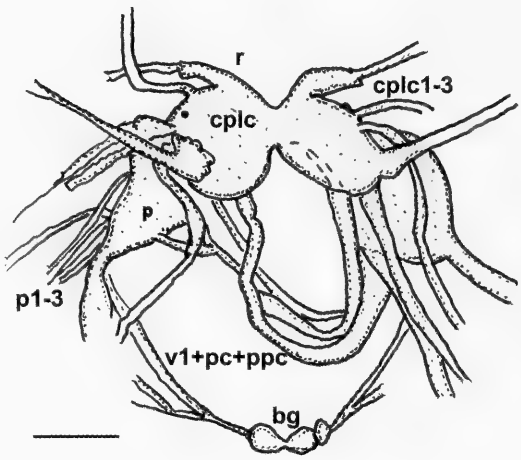


Figure 74. *Aegires minor* (Eliot, 1904). CASIZ 068668. Central nervous system: bg = buccal ganglia, cplc = cerebropleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.75 mm.

Aegires serenae (Gosliner and Behrens, 1997)

(Figs. 75–76)

Notodoris serenae Gosliner and Behrens, 1997: 303–307, Figs 7C, 12A–C, 13.
Aegires serenae (Gosliner and Behrens) comb. nov.

Type material.— For a complete list of the type material see Gosliner and Behrens (1997).

Material examined.— Paratype: CASIZ 107229, two specimens; one specimen 57 mm, dissected. Madang, Papua New Guinea, collected August 1989, T. Gosliner and D. Behrens.

Distribution.— Belau, Papua New Guinea, Philippines, Indonesia, Malaysia, Pohnpei, Guam, and Okinawa (Gosliner and Behrens 1997; C. Carlson and P.J. Hoff, pers. commun.).

Digestive system.— *Aegires serenae* shares the same general digestive anatomy as other *Notodoris* species (Fig. 67B). The buccal bulb is nearly round (Fig. 75) with four large muscles attached, two per side. The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thin cuticle. The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland.

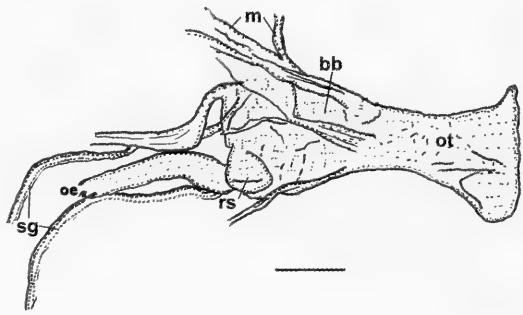


Figure 75. *Aegires serenae* (Gosliner and Behrens, 1997). CASIZ 107229. Buccal bulb: bb = buccal bulb, m = muscles, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 2 mm.

Central nervous system.— As with other species of *Aegires* (formerly *Notodoris*),

the cerebral and pleural ganglia are fused together (Fig. 76). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cerebral ganglia by two relatively long nerves as compared to most other *Aegires*. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

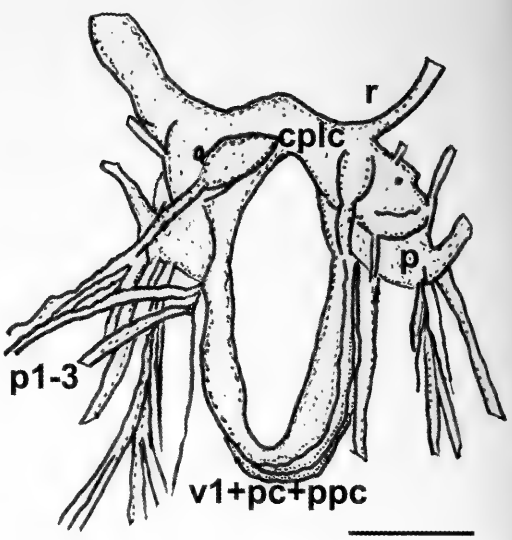


FIGURE 76. *Aegires serenae* (Gosliner and Behrens, 1997). CASIZ 107229. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 1 mm.

REMARKS.— Gosliner and Behrens (1997) have recently described this Indo-Pacific species. Anatomical information for the present study has been taken from their paper. However, they did not describe some characters that were necessary for the present study such as the central nervous system and the digestive systems. Therefore, the additional specimens noted above were examined to complete the data.

Taxon formerly included in the Genus *Triopella* Sars, 1878

TYPE SPECIES: *Triopella incisa* Sars, 1878:310, by monotypy.
(Figs. 77–81)

Aegires incisus (Sars, 1878)

Triopella incisa Sars, 1878:310, pl. 27, Fig. 3.
Aegires incisus (Sars, 1878) comb. nov.

DIAGNOSIS.— Sars' (1878) partial description is as follows: "Small body, oblong and angled, elongate spicules throughout the dorsum. At the posterior end of the mantle are two lobes. The dorsum is highly arched, having superficial dorsal appendages, and longitudinal medial ridges that converge between the tentacles (rhinophores). At the base of the rhinophores there is a single, large tubercle, with 5–7 smaller tubercles arranged longitudinally along the two medial ridges. There are two small tubercles on the anterior of the dorsum. The oral tentacles are inconspicuous. Dorsal rhinophores are short, perfoliate and retractable. The gill has 3 small and sparse branchae, which are arranged in a semi-circle around the anus. The anus is not completely round. The radula has no rachidian tooth, nor denticulate lateral teeth."

TYPE MATERIAL.— This species was collected from the Norwegian Arctic Sea. No additional collection data are available. Type material not found in the collections at the Natural History Museum, Oslo.

MATERIAL EXAMINED.— D 15983, two specimens, 8–9 mm, Bodø, Norway; D 15988, two specimens, 6–8 mm, Sande Fjord, Norway. No additional collection data are available.

DISTRIBUTION.— Norway and Greenland (Sars 1878; Norman 1893; Odhner 1922; Marcus

and Marcus 1969). This species has been mentioned several times in the literature (Fischer 1880–1887; Bergh 1883, 1892; Norman 1893; Odhner 1907; Eliot 1910a; Thiele 1929–31; Odhner 1939).

External morphology.— The specimens examined for the present study match the previously published description and drawings mentioned above. A drawing of one of the preserved specimens from the type locality is presented in Figure 77.

Digestive system.— *Aegires incisus* shares the same general digestive anatomy as other Aegiridae species (Figs. 3B, 8B). The esophagus is short and connects directly to the stomach. The intestine makes a simple, wide curve along the outside of the digestive gland. The buccal bulb is nearly round, with four large muscles attached, two per side (Fig. 78). The buccal bulb is shorter and more round than the oral tube. The radular sac slightly protrudes from the bulb, under the esophagus. The labial disk frames the triangular opening to the buccal bulb and is lined with a thick cuticle. There is a thick jaw plate at the top of the opening, with thick rods at the edge (Fig. 79A). The radular formula is 13 × 16.0.16. The teeth are simply hamate and the two innermost lateral teeth are smaller than the remaining teeth (Figs. 79B–D).

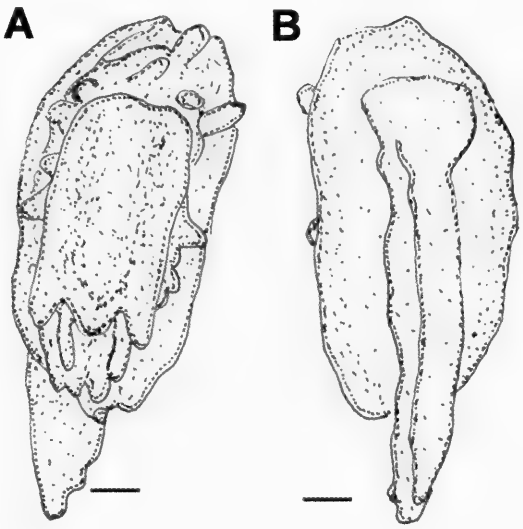


Figure 77. *Aegires incisus* (Sars, 1878). NMNH D15988. Drawing of preserved specimen. (A) Dorsal view. (B) Ventral view. Scale = 0.8 mm.

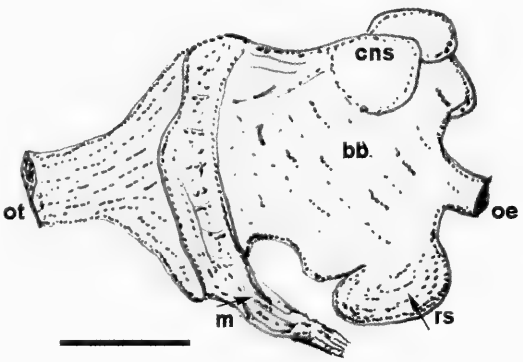


Figure 78. *Aegires incisus* (Sars, 1878). NMNH D15988. Buccal bulb: bb = buccal bulb, m = muscles, oe = esophagus, ot = oral tube, rs = radular sac, sg = salivary glands, scale = 0.6 mm.

Reproductive system.— The reproductive system is triaulic (Fig. 80). The ampulla is large and bulbous at the distal end and tubular at the proximal end. It branches into the oviduct and the prostate. The prostate is wide and narrows before broadening again in the central portion. It narrows before entering into the long sausage-shaped deferent duct. The deferent duct leads to the penis, which is only slightly bulbous at the distal end. There are densely packed hooks along the length of the penis. The vagina is very wide and was not examined internally. Thus the presence of spines or hooks cannot be confirmed. The vaginal duct is extremely wide and short and at the proximal end, enters the bursa copulatrix. The bifurcating oviduct that originates from the very elongate receptaculum seminis enters the vagina. The oviduct enters the female gland mass. The bursa is round and small.

Central nervous system.— The cerebral and pleural ganglia of *Aegires incisus* are fused together (Fig. 81). The two pedal ganglia are located below the cerebro-pleural complex and are joined by the pedal commissure, the parapedal commissure and the visceral loop. The buccal ganglia are located under the esophagus, below the central nervous system. They are joined to the cere-

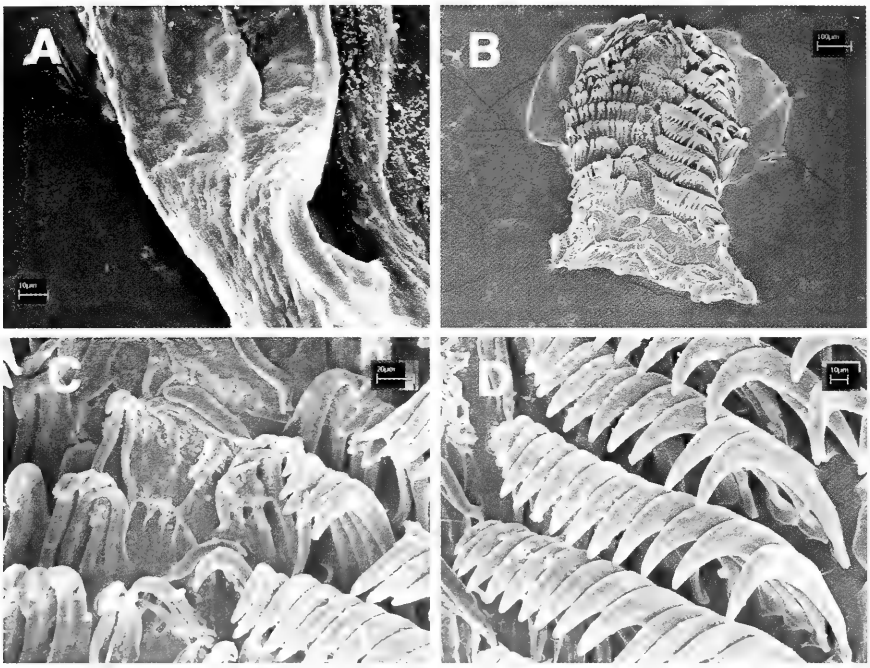


FIGURE 79. *Aegires incisus* (Sars, 1878). NMNH D15988. Buccal morphology: (A) Jaw, scale =10 μm. (B) Whole radula, scale = 100 μm. (C) Inner lateral teeth, scale = 20 μm. (D) Outer lateral teeth, scale = 10 μm.

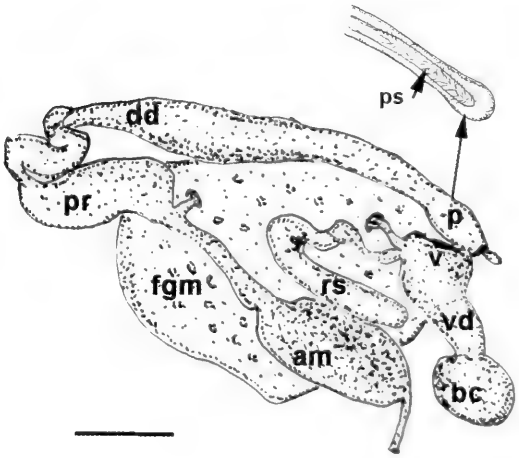


FIGURE 80. *Aegires incisus* (Sars, 1878). NMNH D15988. Reproductive system: am = ampulla, bc = bursa copulatrix, dd = deferent duct, fgm = female gland mass, p = penis, pr = prostate, ps = penial spines, rs = receptaculum seminis, v = vagina, vd = vaginal duct, scale = 0.3 mm.

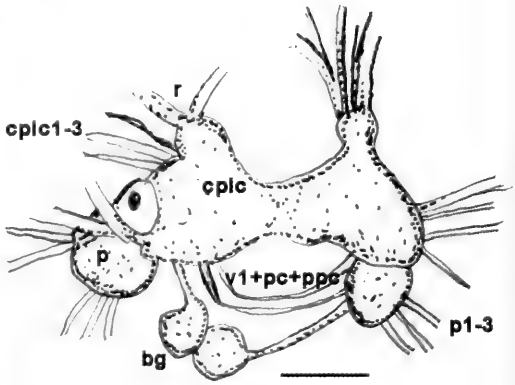


FIGURE 81. *Aegires incisus* (Sars, 1878). NMNH D15988. Central nervous system: bg = buccal ganglia, cplc = cerebro-pleural ganglia complex, p = pedal ganglia, r = rhinophoral nerve, vl+pc+ppc = visceral loop, scale = 0.67 mm.

bral ganglia by two relatively short nerves. There are four cerebral nerves leading from each cerebral ganglion, and three large pleural nerves leading from the right and left pleural ganglia. There is a separate abdominal ganglion on the right side of the visceral loop. Gastro-esophageal, rhinophoral and optical ganglia are present.

Circulatory system.— (not shown) The heart is relatively small as compared to most cryptobranch dorids (Valdés 2002). There is one blood gland situated in front of and to the right side of the visceral cavity.

Remarks.— *Aegires incisus* (formerly *Triopella incisa*) has been often overlooked as a species of Aegiridae as discussed in the earlier section on the history of the classification. However, the species examined from the type locality can be confirmed as *Triopella incisa* Sars, 1878 from the drawings and descriptions provided by Sars and subsequent collectors. Phylogenetic analyses performed for the present study using 58 of the 64 considered morphological characters indicate that *T. incisa* is the sister species of *Aegires sublaevis*. Therefore, *Triopella* cannot be maintained as a separate taxon without rendering *Aegires* paraphyletic. We propose to unite *Triopella incisa* with the *Aegires* with the name *Aegires incisus* (Sars, 1878). Further details are provided in the phylogenetic analysis below.

Phylogenetic Analysis

The outgroup taxa chosen for the present analysis are discussed in a prior section, Material and Methods. Character states for *Bathydoris abyssorum* were taken from the literature (Bergh 1884; Gosliner and Bertsch 1988; Wägele 1989; Cervera et al. 2000; Valdés 2002). Character states for the additional outgroups were taken both from the literature and from museum material when available. Table 3 (see Appendix) summarizes the information for the outgroup taxa. Morphological data were organized using MacClade, ver 3 (Maddison and Maddison 1998).

Characters.— The following characters were considered for use in the analyses of Aegiridae. The character states are indicated as follows: 0: the presumed plesiomorphic condition; 1,2,3: apomorphic condition. For character states that are not applicable, "-" is used and for missing data, "?" is used. The distribution of plesiomorphic and apomorphic character states is presented in Table 2 (see Appendix). Character states for the taxa examined for the present study can be found in Table 4 (see Appendix). "Outgroup taxa" refers to the combination of *Bathydoris,* the six phanerobranchs, the three cryptobranchs and *Hexabranchus*. Only the generic name is used for the outgroup taxa. "Ingroup taxa" refers to all *Aegires,* including those taxa formerly known as *Notodoris* and *Triopella*.

1. *Body shape*: Wide with a distinct mantle (0): all outgroup taxa except for *Holoplocamus*, *Okenia* and *Polycera*. Elongate with a reduced/absent margin (1): all ingroup taxa.
2. *Dorsal ridges*: Absent (0): all outgroup taxa and most ingroup taxa. Present (1): *Aegires albopunctatus, A. palensis, A. punctilucens, A. sublaevis* and *Triopella incisa*.
3. *Dorsal features*: Autotomizable (0): *Bathydoris*. Permanent (1): all other outgroup and ingroup taxa. This character is not applicable to *Hexabranchus*, which does not have dorsal features.
4. *Permanent features*: Low (0): all outgroup taxa except *Holoplocamus* and *Okenia* and over half the ingroup taxa. Elevated (1).
5. *Dorsal feature shape*: Rounded (0): All outgroup taxa and two-thirds of the ingroup species. Flattened (1): one-third of the ingroup taxa.
6. *Tubercles*: Scattered (0): All outgroup taxa except *Okenia* and *Polycera* and over half the ingroup taxa. In rows (1): nearly half the ingroup taxa.
7. *Rhinophores*: Not retractable (0): *Bathydoris* and *Okenia*. Retractable (1): all other taxa.
8. *Rhinophore lamellae*: Transverse or longitudinal (0): all outgroup taxa except *Conualevia*. Smooth (1): all ingroup taxa and *Conualevia*.
9. *Rhinophore pocket*: Simple hole, slit (0): all outgroup taxa except *Hexabranchus*. Raised (1): all ingroup taxa.
10. *Rhinophore tubercles*: None (0): all outgroup taxa. Outer marginal only (1): all ingroup taxa except for *A. palensis, A. punctilucens* and *A. exeches* which all have character state 2. All around (2).

11. *Rhinophore tubercle number*: None (0): all outgroup taxa. Three to five (1): half the ingroup taxa. One tubercle (2): half the ingroup taxa. This character was not included in the final analyses because the character states are included in other characters (#10).
12. *Oral tentacles/hood*: Tentacles (0): *Bathydoris, Calycidoris, Conualevia, Hexabranchus*, and *Holoplocamus*. Oral hood/veil (1): no ingroup taxa have an oral hood or veil. Neither (2): all remaining outgroup taxa and all ingroup taxa.
13. *Oral tentacle size*: Large (0): *Bathydoris* and *Hexabranchus*. Short/small (1): *Conualevia* and *Holoplocamus*. This character is not applicable for the ingroup taxa.
14. *Integumentary spicules*. Present (0): *Actinocyclus, Bathydoris, Hexabranchus, Holoplocamus* and *Polycera*. Absent (1): all other outgroup taxa and all ingroup taxa.
15. *Gill retraction*: Contractile (0): all ingroup taxa and *Bathydoris*, *Holoplocamus*, *Okenia*, and *Polycera*. Retractile (1): all other outgroup taxa.
16. *Gill branches*: Few (0): Most ingroup taxa and *Bathydoris*, *Diaphorodoris*, and *Holoplocamus*. Numerous (1): all remaining outgroup and ingroup taxa.
17. *Gill leaf ramification*: Multi-pinnate (0): *Bathydoris*, *Hexabranchus*, *Holoplocamus*, and *Mandelia*. Not multi-pinnate (1): all other outgroup and ingroup taxa.
18. *Gill arrangement*: Isolated points (0): *Bathydoris*, *Diaphorodoris*, *Hexabranchus*, and *Onchidoris*. One opening (1): all other outgroup and ingroup taxa.
19. *Gill protective structures*: Large, firm (0): all *Notodoris* and *A. hapsis*. Tubercles (1): *Holoplocamus* and half the ingroup taxa. Elongate appendages (2): all remaining *Aegires* species. This character was not included in the final analyses because the character states are included in other characters (#20, #61).
20. *Gill protective structures*: Simple (0): *Holoplocamus* and over half the ingroup taxa. Compound, ramified (1): the remaining ingroup taxa.
21. *Buccal pump*: Absent (0): all ingroup taxa and most outgroup taxa. Present (1): remaining taxa.
22. *Oral glands*: Absent (0): most taxa included in the study. Present (1): *A. villosus, A. malinus, A. incusus*, and *A. hapsis*.
23. *Jaw rodlets*: Absent (0): half the taxa included in the study. Present (1): half the taxa included in the study.
24. *Jaws*: Thick, chitinous (0): *Bathydoris*, *Okenia*, *Polycera* and most ingroup taxa. Thin (1): remaining outgroup taxa except *Mandelia* and all *Notodoris*. Absent (2): *Mandelia*.
25. *Rachidian*: Present (0): *Bathydoris* and *Onchidoris*. Absent (1): all remaining taxa included in the study.
26. *Lateral teeth size*: Outer smallest (0): *Bathydoris* and *Calycidoris*. Inner smallest (1): most ingroup taxa and remaining outgroup taxa. Both small (2): *Conualevia*, *A. albus*, *A. punctilucens*, *Triopella incisa*, and *N. citrina*.
27. *Inner lateral teeth shape*: Elongate (0): *Actinocyclus* and *Bathydoris*. Hamate (1): *Conualevia, Hexabranchus, Holoplocamus, Polycera* and most ingroup taxa . Hooked (2): *Calycidoris*, *Diaphorodoris*, *Okenia*, *Onchidoris*, *A. incusus*, and *A. hapsis*.
28. *Second lateral tooth*: Same size as inner (0): all taxa examined except *Actinocyclus*, *Diaphorodoris*, *Okenia*, and *Onchidoris*. Markedly reduced (1).
29. *Outer lateral tooth*: Present (0): all taxa examined except *Calycidoris*, *Diaphorodoris*, *Okenia*, *Onchidoris*, and *Polycera*. Absent (1).
30. *Outer lateral teeth shape*: Hooked (0): all taxa included in the study except for *Actinocyclus* and *Holoplocamus*. Not hooked (1).
31. *Radular teeth denticulation*: No denticles (0): *Bathydoris*, *Conualevia*, *Holoplocamus*, *Polycera*, and all *Aegires* species. One spur below main cusp (1): all *Notodoris*. Denticulate (2):all remaining outgroup taxa.
32. *Reproductive system*: Diaulic (0) *Bathydoris*. Triaulic (1): all remaining species in the study.
33. *Vagina shape*: Elongate/thin (0): all outgroup taxa except *Diaphorodoris* and *Okenia* and two-thirds of the ingroup species. Wide, bulbous (1): one-third of the ingroup taxa. This character was not included in the final analyses because the state could not be confirmed in several taxa.
34. *Ampulla shape*: Elongate, sausage-shaped (0). Rounded, bulbous (1).
35. *Penis*: Same width as deferent duct (0): all outgroup taxa except *Hexabranchus*, *Mandelia, Okenia*, and *Onchidoris* and over half the ingroup taxa. Wider than deferent duct (1): the remaining ingroup species.
36. *Penial hooks*: Absent (0): *Actinocyclus*, *Bathydoris*, *Conualevia*, *Hexabranchus*, and *Mandelia*. Present

(1): remaining outgroup taxa and all ingroup taxa.

37. *Penial hooks*: Few (0): all outgroup taxa. Many (1): all ingroup taxa. This character was not included in the final analyses because it is the same character as #39.
38. *Penial spines*: Throughout (0): all outgroup taxa and six ingroup taxa. Distal tip only (1): most ingroup taxa.
39. *Penial spines*: Sparse (0): all outgroup taxa. Dense (1): all ingroup taxa.
40. *Vestibular gland*: Absent (0): all taxa included in the present study except *Aegires sublaevis*. Present (1).
41. *Bursa copulatrix ducts*: One duct (0): *Actinocyclus*, *Bathydoris*, *Holoplocamus* and one-third of the ingroup taxa. Two ducts (1): the remaining outgroup taxa and two-thirds of the ingroup species.
42. *Pleural ganglia*: Differentiated (0): *Bathydoris*. Fused with cerebral ganglia (1): all remaining outgroup taxa and all ingroup taxa.
43. *Cerebral ganglia*: Two ganglia on each side (0): *Bathydoris*. Fused (1): all remaining outgroup taxa and all ingroup taxa.
44. *Cerebral nerve number*: Three (0): *Bathydoris*. Four or more (1): all remaining outgroup taxa and all ingroup taxa..
45. *Eyes: Absent* (0): *Bathydoris*. Present (1): all remaining outgroup taxa and all ingroup taxa..
46. *Eye position*: Stalks (0): *Actinocyclus*, *Hexabranchus*, and *Holoplocamus*. Prominent (1): all remaining outgroup taxa and all ingroup taxa except *Notodoris*. Not prominent (2): *Notodoris*.
47. *Ganglionic tubercles*: Absent (0): all taxa included in the study except *Hexabranchus*. Present (1): *Hexabranchus*.
48. *Inner lateral tooth*: Without secondary cusp (0): all taxa included in the study except *Holoplocamus* and *Polycera*. With secondary cusp (1): *Holoplocamus* and *Polycera*.
49. *Gill pocket*: Absent (0): all taxa included in the study except *Actinocyclus*, *Conualevia*, and *Mandelia*. Present (1): *Actinocyclus*, *Conualevia*, and *Mandelia*.
50. *Inner two lateral teeth*: Not elongate (0): all taxa included in the study except *Holoplocamus* and *Polycera*. Elongate (1): *Holoplocamus* and *Polycera*.
51. *Foot corners*: Rounded (0): all taxa included in the study except *Holoplocamus* and *Polycera*. Prolonged (1): *Holoplocamus* and *Polycera*.
52. *Foot dimension*: Same as mouth (0): all taxa included in the study except *Actinocyclus, Conualevia*, and *Mandelia*. Narrower than mouth (1): *Actinocyclus*, *Conualevia*, and *Mandelia*.
53. *Rhinophore stalk*: Long (0): all taxa included in the study except *Actinocyclus*, *Conualevia*, *Diaphorodoris*, *Hexabranchus*, and *Mandelia*. Short (1): *Actinocyclus*, *Conualevia*, *Diaphorodoris*, *Hexabranchus*, and *Mandelia*.
54. *Dorsal pigment*: No dark pigment (0): most outgroup taxa except *Actinocyclus, Calycidoris*, *Mandelia*, and *Onchidoris*. This character is applicable for over half the ingroup taxa. Dark pigment (1): remaining outgroup and ingroup taxa.
55. *Dorsal pigment*: Spots (0): all taxa in the study for which this character is applicable except for *Notodoris minor*. Lines (1): *Notodoris minor*.
56. *Dorsal tubercle pigment*: None (0): all outgroup taxa except *Actinocyclus* and *Polycera*. Most ingroup taxa. Dark apex (1): *Actinocyclus*, *Polycera* and seven ingroup species.
57. *Dorsal ocellae*: Absent (0): all outgroup taxa and most ingroup taxa. Present (1): *Aegires pruvotfolae*, *A. punctilucens*, *A. sublaevis*, *A. incusus*, and *A. exeches*.
58. *Dorsal rings*: Absent (0): all outgroup tax except Mandelia and most ingroup taxa. Present (1): *A. pruvotfolae*, *A. sublaevis*, and *A. incusus*. This character was not included in the final analyses because the states are included in character #57.
59. *Rhinophore color*: No dark pigment (0): all ingroup taxa except *A. ortizi*, *A. palensis*, *A. punctilucens*, *A. sublaevis*, and *A. malinus*. Dark rings (1): *Aegires ortizi*, *A. punctilucens*, and *A. sublaevis*. Dark specks (2): *A. palensis* and *A. malinus*.
60. *Rhinophore color*: same as body (0): all outgroup taxa except Calycidoris and most ingroup taxa. Different color from body (1): *Calycidoris*, *A. albopunctatus*, *Notodoris serenae*, *A. ninguis*, *A. malinus*, *A. incusus*, and *A. hapsis*.
61. *Gill protective structures*: Simple, digitform (0): one-third of the ingroup taxa. Same as dorsal tubercles

(1): one-third of the ingroup taxa. Compound structures (2): the remaining third of the ingroup taxa. Fan-shaped (3): only *A. flores*.

62. *Dorsal webbing*: Absent (0): all taxa included in the study except *A. malinus* and *A. hapsis*. Present (1): *Aegires malinus* and *A. hapsis*.
63. *Finger-like structures*: Simple (0): only four ingroup taxa for which this character is applicable. Lobed (1): only *A. albopunctatus* and *A. lemoncello*.
64. *Dorsal spicules*: Smooth (0): most taxa for which this character is applicable. Furry appearance (1): only *A. malinus* and *A. hapsis*. This character was left out of the final analyses because there were not enough data for the taxa included in the study.

Results.— Three most parsimonious trees were obtained with 175 steps and had a consistency index (CI) of 0.38, a retention index (RI) of 0.60 and a homoplasy index (HI) of 0.62. All trees were found in one tree island. The strict consensus tree is shown in Fig. 82A. A majority rule tree from the 3 trees was produced and is shown in Fig. 82B with the character numbers and character reversals. The underlined numbers indicate reversals. The trees indicate that the Aegiridae: *Aegires*, *Notodoris* and *Triopella* form a monophyletic clade and that *Triopella* is nested in a derived clade of *Aegires*. *Notodoris* is nested within *Aegires*. *Bathydoris* is the most basal taxon to the study group. The phanerobranchs included in the analysis are basally situated to Aegiridae and the cryptobranchs included in the study form a sister clade to some suctorian phanerobranchs. A Bremer support analysis shows that most of the clades are poorly supported (Fig. 82A), with the exception of the clade of species formerly known as *Notodoris* and the outgroups.

Analyses performed using *Bathydoris* and the phanerobranchs as outgroups resulted in 6 most parsimonious trees with the same tree scores (trees not shown). The only differences between these trees and those found when using only *Bathydoris* as the outgroup were at the terminal branches. That is, all the deeper nodes remained the same but two polytomies were unresolved: one for all the phanerobranchs other than *Aegires* and one polytomy at the node containing *A. pruvotfolae* and *A. incusus*.

Discussion

The results from our phylogenetic analysis of Aegiridae support the monophyly of Aegiridae. Additionally, the phanerobranch and the cryptobranch dorids examined for the present study form monophyletic sister clades (Fig. 82). In our strict consensus tree (Fig. 82A) the cryptobranch clade containing *Mandelia, Conualevia* and *Actinocyclus* is closely related to the phanerobranchs examined for the present study: *Onchidoris, Diaphorodoris* and *Calycidoris*. Valdés (2002) showed the cryptobranchs as more derived than the phanerobranchs, including *Aegires*. Specifically, Valdés' phylogeny shows *Aegires* as the most basally situated taxon in his study group, with the cryptobranchs and *Hexabranchus* more derived than *Aegires*. This differs from our results that show *Hexabranchus* as the most basally situated taxon to the clade containing all other taxa examined and *Aegires* as the most derived clade.

Valdés' phylogeny also suggests that phanerobranchs are not monophyletic and our results support this view. However, the sequence of branching is distinct.

The results of the present study also show that *Holoplocamus* and *Polycera* are more closely related to each other and more basally situated to the remaining phanerobranchs and cryptobranchs. Characters that unite this clade are body shape (#1), inner lateral teeth with a secondary cusp (#48), elongate inner two lateral teeth (#50), and prolonged foot corners (#51).

Character mapping also revealed interesting relationships between the suctorians and the cryptobranchs. For example, retractile gills (#15) is the apomorphic state shared by the cryptobranchs and suctorians except for *Okenia*. This indicates that the suctorians are the sister group to the cryp-

tobranchs. In the non-suctorians, the gill is truly non-retractile indicating that this character state has been secondarily derived.

The synapomorphies that unite all *Aegires* (including *Notodoris* and *Triopella*) are the absence of rhinophore lamellae (#8), the presence of rhinophore tubercles only on the outer margin (#10) and the presence of many penial spines (#39).

Our analysis shows that within the study group Aegiridae, there are two major *Aegires* clades. One contains the taxa not found in tropical Indo-Pacific seas. The species in this clade (*Aegires albopunctatus, A. palensis, A. punctilucens, A. sublaevis, A. gomezi, A. ortizi* and *Triopella incisa*) are found only from the Mediterranean, northern Europe, the Caribbean and the west coast of North America. The synapomorphy that supports this clade is dorsal tubercles arranged in rows (#6). The second clade containing *Aegires albus,* found in the Antarctic, is also basally situated but more closely related to the tropical Indo-Pacific clade that contains all other *Aegires* species and all former *Notodoris* species. This Indo-Pacific clade is united by a reproductive synapomorphy, penis wider than the deferent duct (#35). *Notodoris* clusters together in a monophyletic clade that is basally situated to the Indo-Pacific *Aegires*. Synapomorphies that unite the *Notodoris* clade are the presence of large, firm gill protective structures (#19), radular teeth that have one spur below the main cusp (#31) and reduced eyes (#46). In all analyses performed for the present study, the *Notodoris* clade is nested within the *Aegires* sharing multiple synapomorphies with *Aegires* (see Fig. 82B).

The name *Aegires* Lovén, 1844 is the older name having precedence over *Notodoris* Bergh, 1875 as discussed in a previous section. Thus, if only considering precedence, the names of the four *Notodoris* species should be assigned to the genus *Aegires*. The name *Notodoris* has been in general use by both amateurs and scientific researchers to distinguish these four firm bodied nudibranchs from other externally similar nudibranchs (Coleman 1989; Wells and Bryce 1993; Gosliner et al. 1996; Marshall and Willan 1999; Coleman 2001; Rudman 2004). In order to maintain the monophyly of *Aegires* we propose to reassign the four *Notodoris* species to *Aegires*. Thus, *Notodoris citrina* Bergh, 1875 becomes *Aegires citrinus* (Bergh, 1875). *Aegires citrinus* Pruvot-Fol, 1930 must be named *Aegires pruvotfolae* Fahey and Gosliner, 2004, named for Alice Pruvot-Fol who first described *Aegires citrinus* from New Caledonia (1930). The use of a junior homonym is required since the species name *citrinus* is already in use within the Aegiridae (*Aegires citrinus*).

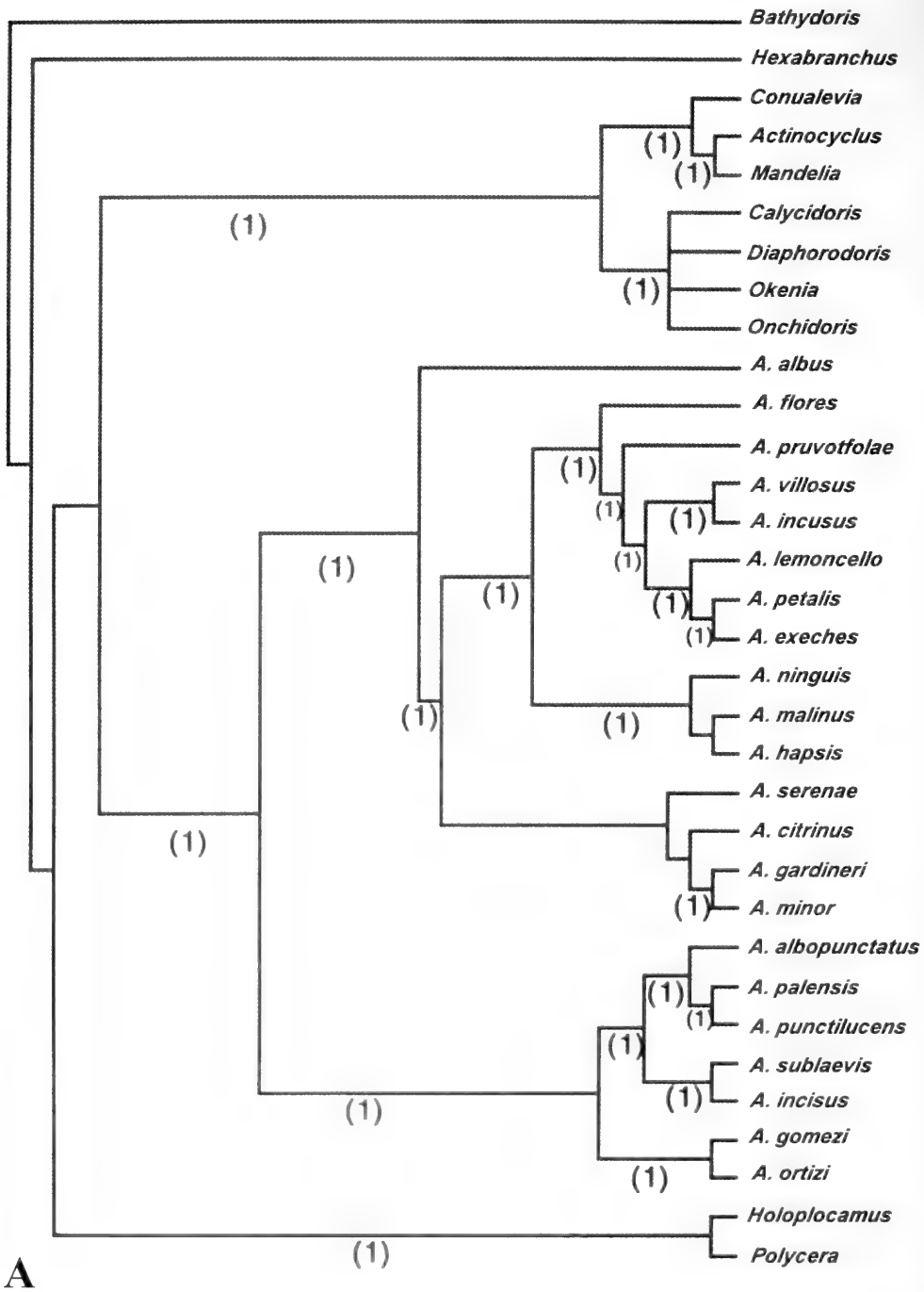
Notodoris gardineri becomes *Aegires gardineri* (Eliot, 1906). *Notodoris minor* is *Aegires minor* (Eliot, 1904) and *N. serenae* is *Aegires serenae* (Gosliner and Behrens, 1997).

With regard to *Triopella incisa*, at this time we propose to name this species *Aegires incisus* (Sars, 1878). Our proposal takes into consideration the following points: this species is firmly nested within the *Aegires* clade in all our analyses, the generic name *Aegires* takes precedence over the name *Triopella* and the lack of general use and recognition of the name *Triopella.*

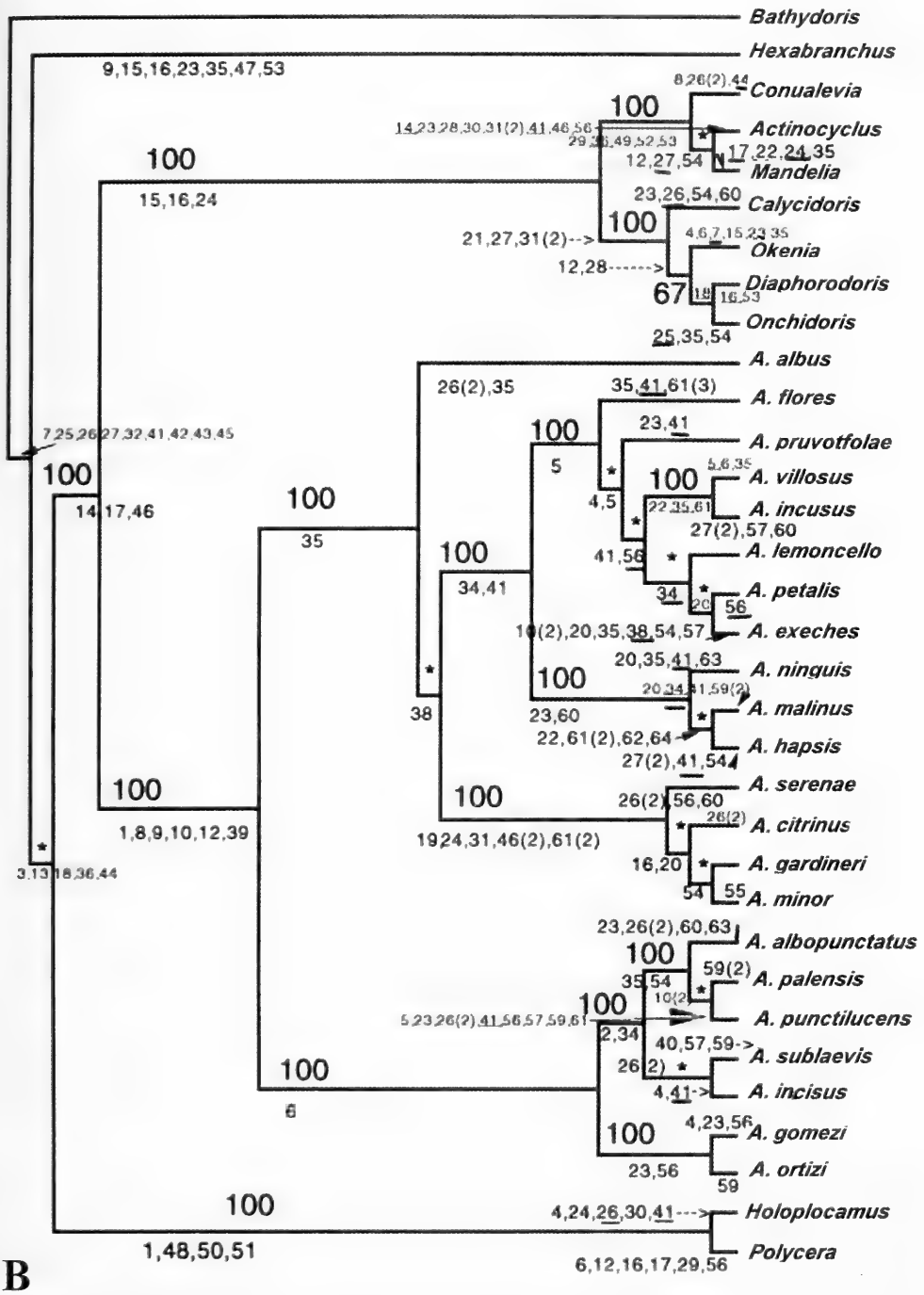
In the present analysis, the traditionally recognized clade Phanerobranchia appears to be paraphyletic and no synapomorphies were found to support the group. Wägele and Willan (2000) and Valdés (2002) also found this to be true. In our analysis, the cryptobranch dorids that we included were nested within the phanerobranchs. Analyses that included only the cryptobranchs and phanerobranchs along with *Aegires albus* also failed to separate the phanerobranchs as a monophyletic clade (tree not shown).

An additional similarity between our analyses and previous studies (Valdés 2002) is the exclusion of *Hexabranchus* from the other cryptobranch or phanerobranch dorids and its placement in a basal position relative to the phanerobranch/cryptobranch clade. Several characters support the position of *Hexabranchus* in the present analysis (Fig. 82B).

In accordance with current perspectives of phylogenetic classification (De Queiroz and



FIGURES 82A–B. Phylogeny of the Aegiridae. (A) (above). Strict consensus tree, 175 steps. Numbers below the branches are Bremer decay values. (B) (right). Majority rule tree of 3 most parsimonious trees. Numbers (100 and 67) above the



branches are the percentage of the 3 consensus trees that agree on this node. The asterisk also denotes 100% agreement on the node. Numbers shown at the branches are character numbers from Table 2. The underlined numbers indicate reversals.

Gauthier 1994) and based on morphological character analysis we propose that the "family group"Aegiridae contains twenty-three species of *Aegires* descendent from a common ancestor.

Biogeographical relationships

The phylogeny of the Aegiridae (Fig. 82) shows a clear-cut case of vicariance and offers some insight into species cladogenesis similar to patterns found in other opisthobranch lineages. There are two conspicuous major clades of *Aegires*. One clade contains 15 species found in the Southern Hemisphere and in the Indo-Pacific tropics while the second clade contains 7 species found in the temperate and tropical Atlantic, the Mediterranean and the temperate eastern Pacific (a Northern Hemisphere clade). In the clade from the Southern Hemisphere and the Indo-Pacific, the most basally situated species, *Aegires albus*, is an Antarctic species and sister taxon to the Indo-Pacific clade. The more numerous taxa are found in the tropical Indo-Pacific with the exception of *A. ninguis* found also from the temperate Indian and Atlantic coasts of South Africa. Given that *A. ninguis* is a derived member of this clade, it is most likely that these species were derived from Indo-Pacific ancestors rather than from other cold water or temperate taxa. One possible explanation for this topology is that there has been a little adaptive radiation of the polar or temperate *Aegires* species similar to *Flabellina* and to a lesser extent *Hallaxa* (Gosliner 1995). The phylogeny of *Aegires* demonstrates a considerable degree of speciation within the Indo-Pacific tropics.

Another possible scenario for the distribution pattern seen for this clade of *Aegires* is that *A. albus* is the last surviving species of a group of cold water *Aegires*. Other cold water or temperate *Aegires* that may have previously existed could have radiated from the colder oceans into the warmer waters of the Indo-Pacific. It is notable that within the clade of the Indo-Pacific species is a small clade of all of the *Aegires* previously known as *Notodoris*. This clade is basally situated to the remaining species and has representative species found along both coasts of Australia, from as far south as the temperate ocean of Perth, Western Australia and extending to latitudes north of the equator. This would provide some evidence for the dispersal of the clade from the Antarctic, north along both coasts of Australia, then into the tropical Indo-Pacific regions.

The second major clade is known primarily from the Mediterranean and along the margin of the eastern Atlantic. Only one species of this clade, *A. albopunctatus*, is found along the temperate eastern Pacific, possibly demonstrating vicariance with the closest sister clade of *A. palensis* and *A. punctilucens* from the Mediterranean. It is also possible that the ranges of these temperate species are incomplete and additional records may show that there is a higher degree of overlap than is currently recognizable.

Finally, species of Aegiridae are extremely small, inconspicuous and infrequently encountered, with the exception of those species previously included in *Notodoris*. It is likely that not all species have yet been described, and further collections may add to our knowledge of the pattern of species cladogenesis and vicariance.

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Appendix

Tables 1–4

TABLE 1. Summary of the historical classification of AEGIRIDAE

Author and Higher level names used	*Genus names included*
1. Alder & Hancock, 1845–1855	
SUBORDERS: p. 36–37	
ANTHOBRANCHES	
Doridídae	
Sub-Family Polycerinae	*Aegires* Lovén, 1844:49
	Thecacera
	Polycera
	Idalia
2. Fischer, 1883	
SUBORDERS: p. 519	
Anthobranchiata	
Aglossa: Doridopsidae	
Glossophora:	
Cryptobranchiata,	
Phanerobranchiata	
POLYCERIDAE: p. 525	
Acanthodoridinae	
Polycerinae	
Aegirinae	*Aegires*
	Triopella Sars, 1878:310
3. Bergh, 1890,1892	
Phanerobranchiata	
Tribe Suctoria	
Tribe Non Suctoria	
POLYCERIDAE	*Aegires*
	Notodoris Bergh, 1875d:64
	Triopella
4. Eliot, 1910	
NOTODORIDIDAE	*Aegires*
	Notodoris
	Triopella
5. Iredale & O'Donoghue 1923	
AEGIRETIDAE	*Aegires*
	Notodoris
	Triopella
6. Thiele, 1929–1935	
POLYCERIDAE	
NOTODORIDINAE p. 696	*Aegires*
	Notodoris
	Triopella
7. Pruvot-Fol, 1954	
PHANEROBRANCHIATA Bergh	
AEGIRETIDAE	*Aegires*
(=Notodoridinae Thiele, 1929-35)	*Notodoris*
8. Fischer et al. 1968	
PHANEROBRANCHIA Fischer, 1883	
Anadoridacea Fischer, 1968	
Tribe Non Suctoria Bergh, 1892:141(1133)	
AEGIRETIDAE Iredale & O'Donoghue 1923	*Aegires*
(= Notodorididae Eliot, 1910)	*Anaegires*
	Notodoris
	Triopella
9. Nordsieck, 1972	
AEGIRETIDAE	*Aegires*
	Anaegires
	Serigea Nordsieck, 1972:55
	Triopella
10. Thompson, 1976	
NOTODORIDIDAE Odhner, 1926	*Aegires*
	Notodoris
11. Rudman, 1998	
AEGIRETIDAE	*Aegires*
	Notodoris

TABLE 2. Characters and states examined for the phylogenetic analysis of Aegiridae. 0 = plesiomorphic; 1,2,3 = apomorphic conditions.

Characters	*States*
1. Body shape	0: wide, distinct mantle; 1: elongate, reduced margin
2. Dorsal ridges	0: absent; 1: present
3. Dorsal features	0: autotomizable 1: permanent
4. Permanent features	0: low; 1: elevated
5. Dorsal feature shape	0: rounded; 1: flattened; 2: pointed, cones
6. Tubercles	0: scattered, 1: in rows
7. Rhinophores	0: not retractable; 1: retractable
8. Rhinophore lamellae	0: transverse or longitudinal lamellae; 1: smooth
9. Rhinophore pocket	0: simple hole/slit; 1: raised
10. Rhinophore tubercles	0: none; 1: outer marginal only; 2: all around
11. Rhinophore tubercle no.	0: many; 1: three to five; 2: one
12. Oral tentacles/hood	0: tentacles; 1: oral hood/veil; 2: neither
13. Oral tentacle size	0: large; 1: short/small
14. Integumentary spicules	0: present; 1:absent
15. Gill retraction	0: contractile; 1: retractile
16. Gill branches	0: few; 1: numerous
17. Gill leaf ramification	0: multi-pinnate; 1: not multi-pinnate
18. Gill arrangement	0: isolated points; 1: one opening
19. Gill protective structures	0: large, firm; 1: tubercles; 2: elongate appendages
20. Gill protective structures	0: simple; 1: compound/ramified
21. Buccal pump	0: absent; 1: present
22. Oral glands	0: absent; 1: present
23. Jaw rodlets	0: absent; 1: present
24. Jaws	0: thick, chitinous; 1: thin; 2: absent
25. Rachidian	0: present; 1: absent
26. Lateral teeth size	0: outer smallest; 1: inner smallest; 2: both small
27. Inner lateral teeth shape	0: elongate; 1: hamate; 2: hooked
28. Second lateral tooth	0: same size as inner; 1: markedly reduced
29. Outer lateral tooth	0: present; 1: absent
30. Outer lateral teeth shape	0: hooked; 1: not hooked
31. Radular teeth denticulation	0: no denticles; 1: one spur below main cusp; 2: denticulate
32. Reproduction system	0: diaulic; 1: triaulic
33. Vagina shape	0: elongate thin; 1: wide bulbous
34. Ampulla shape	0: elongate sausage-shaped; 1: rounded/bulbous
35. Penis	0: same width as deferent duct; 1: wider than deferent duct
36. Penial hooks	0: absent; 1: present
37. Penial hooks	0: few; 1: many
38. Penial spines	0: throughout; 1: tip only
39. Penial spines	0: sparse; 1: dense
40. Vestibular gland	0: absent; 1: present
41. Bursa copulatrix ducts	0: one duct; 1: two ducts
42. Pleural ganglia	0: differentiated; 1: fused with cerebral ganglia
43. Cerebral ganglia	0: two ganglia on each side; 2: fused
44. Cerebral nerve no.	0: three; 1: four or more
45. Eyes	0: absent; 1: present
46. Eye position	0: stalks; 1: prominent; 2: not prominent
47. Ganglionic tubercles	0: absent; 1: present
48. Inner lateral teeth	0: no secondary cusp; 1: with secondary cusp
49. Gill pocket	0: absent; 1: present
50. Inner two lateral teeth	0: not elongate; 1: elongate
51. Foot corners	0: rounded; 1: prolonged
52. Foot dimension	0: same as mouth; 1: narrower than mouth
53. Rhinophore stalk	0: long; 1: short
54. Dorsal pigment	0: no dark pigment; 1: dark pigment
55. Dorsal dark pigment	0: spots; 1: lines
56. Dorsal tubercle pigment	0: none; 1: dark apex
57. Dorsal ocellae	0: absent; 1: present
58. Dorsal rings	0: absent; 1: present
59. Rhinophore color	0: none; 1: dark rings; 2: dark specks
60. Rhinophore color	0: same as body; 1: different from body
61. Gill protective structures	0: simple digitform; 1: same as dorsal tubercles; 2: compound; 3: fan-shaped
62. Dorsal webbing	0: absent; 1: present
63. Finger-like structures	0: simple; 1: lobed
64. Dorsal spicules	0: smooth; 1: furry

TABLE 3. Outgroup species and cryptobranch dorids included in the analysis and source of information

Species	*Literature source*	*Additional material examined*
Actinocyclus verrucosus Ehrenberg, 1831	Ehrenberg, 1831; Valdés and Gosliner, 1999; Valdés, 2002	
Bathydoris abyssorum Bergh, 1884	Wägele, 1989; Valdés, 1999, 2002	
Calycidoris güntheri Abraham, 1876	Abraham, 1876, 1877; Roginskaya, 1972; Valdés, 2002	
Conualevia marcusi Collier and Farmer, 1964	Valdés, 2002; Collier & Farmer, 1964; Valdés, 2002	CASIZ 018370 (1)
Diaphorodoris luteocincta (Sars,1870)	Schmekel & Portmann, 1982; Pruvot-Fol, 1954; Valdés, 2002	CASIZ 072580 (6)
Hexabranchus sanguineus (Rüppell & Leuckart, 1828)	Cuvier, 1804; Valdés, 2002; Ehrenberg, 1831	CASIZ 071704 (1) CASIZ 087263 (1)
Holoplocamus papposus Odhner, 1926	Odhner, 1926; Marcus & Marcus, 1969	Two specimens collected Sept. 1981 by T. Gosliner, Gough Island, Tristan de Cunha Group, So. Atlantic
Mandelia mirocornata Valdés and Gosliner, 1999	Valdés & Gosliner, 1999, 2001	
Okenia elegans (Leuckart 1828)	Pruvot-Fol, 1954; Schmekel & Portmann, 1982; Valdés & Gosliner, 1999	
Onchidoris bilamellata (Linnaeus 1767)	Thompson & Brown, 1984; Valdés, 2002	CASIZ 056306 (6)
Polycera quadrilineata (Müller 1776)	Alder & Hancock, 1851; Schmekel & Portmann, 1982; Thompson and Brown, 1984; Valdés & Gosliner, 1999	CASIZ 074446 (1)

MatrixTest1		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45
1		Body	Dors	Tube	Rhin	Rhin	Rhin	Rhin	Rhin	Oral	Oral	Dors	Dors	JawF	Oute	Inte	GillR	GillB	GillL	GillA	GillB	GillP	Jaws	Rach	Inne	Seco	Oute	Radu	Vagu	Bucc	Ampl	Penis	Penis	Penis	Vest	Bursi	Pleur	Cere	Cere	Eyes	EyeR	Gang	Later	Oral	Repr	gill
1	Actinocyclus	0	0	0	1	0	0	0	-	2	-	0	-	1	0	1	1	1	0	1	-	-	1	1	0	1	1	1	0	0	0	0	0	-	0	1	1	1	1	1	0	0	0	0	1	1
2	Bathydoris	0	0	0	0	0	-	-	0	1	0	0	-	0	0	1	0	0	0	0	-	-	0	0	0	0	0	0	-	0	0	0	0	-	0	0	0	0	0	0	-	0	0	0	0	0
3	Calycidoris	0	0	0	0	0	0	0	0	0	-	1	0	1	1	0	1	1	0	1	-	-	1	1	2	1	-	0	0	1	0	1	1	?	0	0	1	1	?	1	?	0	1	0	1	1
4	Conualevia	0	0	0	1	1	0	2	0	1	1	1	3	0	0	0	1	1	0	1	-	-	1	1	1	0	0	0	0	0	0	1	0	-	0	0	1	1	0	1	1	0	2	0	1	1
5	Diaphorodoris	0	0	0	0	0	0	2	0	0	-	1	0	0	1	0	1	0	0	0	-	-	1	1	2	1	-	2	1	1	0	1	1	?	0	1	1	1	?	1	?	0	1	0	1	1
6	Hexabranchus	0	0	-	1	0	1	0	-	0	-	2	-	1	0	1	1	1	1	0	-	-	0	1	1	0	0	0	0	0	0	1	0	-	0	1	1	1	0	1	0	1	1	0	1	1
7	Mandelia	0	0	0	1	0	0	2	0	2	-	1	1	-	-	0	1	1	1	1	-	-	2	-	-	-	-	-	0	0	0	1	0	-	0	0	1	1	?	1	?	0	-	1	1	1
8	Okenia	1	0	1	0	0	-	-	-	2	-	1	0	1	1	0	0	1	0	1	-	-	1	1	2	1	-	2	1	1	0	1	1	?	0	1	1	1	?	1	?	0	1	0	1	0
9	Onchidoris	0	0	0	0	0	0	0	-	2	-	1	1	0	1	0	1	1	0	0	-	-	1	0	2	1	-	2	0	1	0	?	1	?	0	1	1	1	?	1	?	0	1	0	1	1
10	Polycera	1	0	1	0	0	-	-	-	2	-	0	-	0	1	1	0	1	0	1	-	-	1	1	1	0	0	0	0	0	1	0	1	?	0	1	1	1	?	1	?	0	1	0	1	0
11	A. albus	1	0	0	1	1	1	1	1	2	-	1	1	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	1	-	0	1	1	1	1	1	1	0	1	0	1	0
12	A. albopunctatus	1	0	1	1	1	1	1	1	2	-	1	1	2	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	1	0	1	-	0	1	1	1	1	1	1	0	1	0	1	0
13	A. citrinus	1	0	0	1	1	1	1	2	2	-	1	2	2	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	1	1	1	-	0	0	1	1	1	1	1	0	1	0	1	0
14	A. gomezi	1	0	1	1	1	1	1	2	2	-	1	2	2	0	0	0	0	1	1	1	0	0	1	1	0	0	0	?	0	?	?	?	-	?	?	1	1	1	1	1	0	1	0	1	0
15	A. ortizi	1	0	1	1	1	1	1	2	2	-	1	1	2	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1	-	0	1	1	1	1	1	1	0	1	0	1	0
16	A. palensis	1	1	1	1	1	1	2	1	2	-	1	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	1	1	1	-	0	0	1	1	1	1	1	0	1	0	1	0
17	A. punctilucens	1	0	1	1	1	1	2	1	2	-	1	1	2	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	1	1	?	-	0	0	1	1	1	1	1	0	1	0	1	0
18	A. sublaevis	1	1	-	1	1	1	1	2	2	-	1	1	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	1	0	0	0	?	-	1	1	1	1	1	1	1	0	1	0	1	0
19	A. villosus	1	0	1	1	1	1	1	1	2	-	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	1	0	1	0	0	1	1	1	1	1	1	0	1	1	1	0
20	T. incisa	1	1	1	1	1	1	1	2	2	-	1	1	0	0	0	0	0	1	-	1	1	0	0	1	1	0	0	0	1	0	1	1	?	?	0	0	1	1	1	1	1	0	1	0	1	0
21	N. citrina	1	0	0	1	1	1	1	2	2	-	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	1	1	1	1	1	2	0	2	0	1	0
22	N. gardineri	1	0	1	1	1	1	1	2	2	-	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	1	1	1	1	1	2	0	2	0	1	0
23	N. minor	1	0	0	1	1	1	1	2	2	-	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	1	1	1	1	1	2	0	2	0	1	0
24	N. serenae	1	0	0	1	1	1	1	2	2	-	1	1	0	0	0	0	0	1	1	1	0	1	1	1	1	0	0	1	0	0	0	1	1	0	0	1	1	1	1	1	2	0	2	0	1	0
25	A. ninguis	1	0	0	1	1	1	1	1	2	-	1	1	2	0	0	0	0	1	1	1	0	1	1	1	0	0	0	1	0	1	1	1	0	0	0	1	1	1	1	1	0	1	0	1	0
26	A. lemoncello	1	0	1	1	1	1	1	2	2	-	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	0	0	?	0	1	1	1	1	1	1	0	1	0	1	0
27	A. malinus	1	0	-	1	1	1	1	2	2	-	1	3	2	0	0	0	0	1	1	1	1	1	1	1	0	0	0	0	0	0	1	0	0	0	1	1	1	1	1	1	0	0	1	1	0
28	A. incusus	1	0	1	1	1	1	1	1	2	-	1	2	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	1	1	1	1	0	1	1	1	0
29	A. flores	1	0	0	1	1	1	1	1	2	-	1	2	0	0	0	0	0	1	1	1	0	0	1	1	0	0	0	0	0	0	1	0	1	0	0	0	1	1	1	1	1	0	1	0	1	0
30	A. petalis	1	0	0	1	1	1	1	1	2	-	1	2	0	0	0	0	0	1	1	1	1	0	0	1	1	0	0	0	0	0	0	0	1	0	1	1	1	1	1	1	0	1	0	1	0
31	A. exeches	1	0	1	1	1	1	1	1	2	-	1	2	0	0	0	0	0	1	1	1	1	0	1	1	0	0	0	0	0	0	1	0	1	0	1	1	1	1	1	1	0	1	0	1	0
32	A. hipsus	1	0	0	1	1	1	1	1	2	-	1	3	2	0	0	0	0	1	1	2	0	0	1	1	0	0	0	0	0	1	1	0	?	0	0	1	1	1	1	1	0	2	1	1	0

TABLE 4. Data matrix of character states in the taxa examined for the phylogenetic analysis of Aegiridae. Data codes: 0 = presumed plesiomorphic condition, 1-3 = apomorphic conditions, - = character not applicable, ? = missing data.

Table4F&G 2		34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62	63	64
		Ampl	Poni	Peru	Poni	Peru	poni	Vest	Burs	Pleu	Cero	Cera	Eyes	Eye	Gan	inne	Gill	inne	foot	footd	rhino	Dors	Dors	Dors	Dors	Dors	Rhin	rhino	Gill	Dors	finge	spicu
1	Actinocyclus	0	0	0	-	-	-	0	0	1	1	1	1	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	-	0	-	-
2	Bathydoris	0	0	0				0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	-	0	0	0	0	0	-	0	-	-
3	Calycidoris	0	0	1	0	0	0	0	1	1	1	?	1	?	0	0	0	0	0	0	0	1	0	0	0	0	0	1	-	0	-	-
4	Conualevia	0	0	0				0	1	1	1	0	1	1	0	0	1	0	0	1	1	0	-	0	0	0	0	0	-	0	-	-
5	Diaphorodoris	0	0	1	0	0	0	0	1	1	1	?	1	?	0	0	0	0	0	0	1	0	-	0	0	0	0	0	-	0	-	-
6	Hexabranchus	0	1	0	-	-	-	0	1	1	1	0	1	0	1	0	0	0	0	0	1	0	-	-	0	0	0	0	-	0	-	
7	Holoplocamus	0	0	1	0	0	0	0	0	1	1	1	1	0	0	1	0	1	1	0	0	0	-	0	0	0	0	0	-	0	-	-
8	Mandelia	0	1	0	-	-	-	0	1	1	1	1	1	1	0	0	1	0	0	1	1	1	0	0	0	1	0	0	-	0	-	-
9	Okenia	0	1	1	0	0	0	0	1	1	1	?	1	?	0	0	0	0	0	0	0	0	-	0	0	0	0	0	-	0	-	-
10	Onchidoris	0	1	1	0	0	0	0	1	1	1	?	1	?	0	0	0	0	0	0	0	1	0	0	0	0	0	0	-	0		-
11	Polycera	0	0	1	0	0	0	0	1	1	1	?	1	?	0	1	0	1	1	0	0	0	-	1	0	0	0	0	-	0		-
12	A. albus	0	1	1	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0
13	A. albopunctatus	1	1	1	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0	1	0
14	A. citrinus	1	0	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	1	0	0	1	0	-	0
15	A. gomezi	0	0	1	1	0	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	1	0	0	0	0	0	0		0
16	A. ortizi	?	?	?	?	?	?	?	?	1	1	1	1	1	0	0	0	0	0	0	0	0	-	1	0	0	1	0	0	0	-	0
17	A. palensis	1	1	1	1	?	?	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	0
18	A. punctilucens	1	1	1	?	?	?	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	1	0	1	0	-	0
19	A. sublaevis	1	0	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	1	1	1	0	0	0	0	0
20	A. villosus	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	1	0	0	0	0	1	0	-	0
21	T. incisa	1	0	1	1	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	0	0	0	0
22	N. citrina	0	1	1	1	1	1	0	1	1	1	1	1	2	0	0	0	0	0	0	0	0	-	0	0	0	0	0	2	0	-	0
23	N. gardineri	0	1	1	1	1	1	0	1	1	1	1	1	2	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0	-	0
24	N. minor	0	1	1	1	1	1	0	1	1	1	1	1	2	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0	-	0
25	N. serenae	0	1	1	1	1	1	0	1	1	1	1	1	2	0	0	0	0	0	0	0	0	-	1	0	0	0	1	2	0	-	0
26	A. ninguis	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0	1	0	0	1	0
27	A. lemoncelio	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	1	0	0	0	0	1	0	-	0
28	A. malinus	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	0	2	1	2	1	-	1
29	A. incusus	1	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	1	1	1	0	1	1	0	-	0
30	A. flores	1	1	1	1	1	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	3	0	-	0
31	A. petalis	0	0	1	1	1	1	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	-	0	0	0	0	0	1	0	-	0
32	A. exeches	0	1	1	0	0	-	0	1	1	1	1	1	1	0	0	0	0	0	0	0	1	0	1	1	0	0	0	1	0	-	0
33	A. hapsis	1	0	1	?	?	?	0	0	1	1	1	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	1	2	1	-	1

TABLE 4 (continued). Data matrix of character states in the taxa examined for the phylogenetic analysis of Aegiridae. Data codes: 0 = presumed plesiomorphic condition, 1-3 = apomorphic conditions, - = character not applicable, ? = missing data.

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Acanthaceae of Sonora: Taxonomy and Phytogeography

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Forty-one species in 15 genera of Acanthaceae are treated from the Mexican state of Sonora. Only a single species (*Tetramerium yaquianum*) is endemic to the state, but 14 others occur only in Sonora and surrounding states and are considered as regional endemics. The occurrences of three species (*Carlowrightia texana, Ruellia leucantha*, and *R. parryi*) in Sonora are reported for the first time. Three Acanthaceae collected in Sonora (*Justicia spicigera, Odontonema cuspidatum*, and *Ruellia malacosperma*) are possibly not native there. A new name, *Justicia hilsenbeckii*, is proposed for the species previously treated as *Siphonoglossa mexicana*. Lectotypifications are designated for five names that pertain to Sonoran plants: *Anisacanthus thurberi, Jacobinia mexicana, Ruellia malacosperma, R. nudiflora*, and *R. parryi*. Sonoran Acanthaceae occur in the following biotic communities (number of species): Sonoran desertscrub (17), Chihuahuan desertscrub (5), thornscrub (21), tropical deciduous forest (23), grasslands (10), oak-pine woodland and/or forest (15). Descriptions of taxa, distribution maps, illustrations of macromorphological features, images of pollen, local names, economic uses, flowering periods, and taxonomic and nomenclatural discussions are provided where appropriate.

Resumen

Se presenta un tratado de 41 especies en 15 géneros de la familia Acanthaceae del estado de Sonora, México. Solamente una especie (*Tetramerium yaquianum*) es endémica al estado, pero 14 especies se consideran endémicas regionales por ocurrir sólo en Sonora y estados adyacentes. Se reportan por primera vez 3 especies nuevas para Sonora: *Carlowrightia texana, Ruellia leucantha*, y *R. parryi*. Tres especies colectadas en Sonora: *Justicia spicigera, Odontonema cuspidatum*, y *Ruellia malacosperma* es probable que no son nativas del estado. Se propone un nombre nuevo: *Justicia hilsenbeckii* para la especie tratada anteriormente como *Siphonoglosa mexicana*. Se presentan lectotipificaciones para 5 nombres de las plantas de Sonora: *Anisacanthus thurberi, Jacobinia mexicana, Ruellia malacosperma, R. nudiflora* y *R. parryi*. Las especies de Acanthaceae en Sonora se distribuyen en las siguientes comunidades bióticas: matorral desértico Sonorense (17), matorral desértico Chihuahuense (5), matorral espinoso (21), selva baja caducifolia (23), pastizales (10), bosque abierto y/o bosque cerrado de pino-encino (15). De acuerdo a la especie, se presentan: descripciones de taxa, mapas de distribución, ilustraciones de características macromorfológicas, imágenes de polen, nombres locales, usos económicos, períodos de floración y discusiones taxonómicas y de nomenclatura.

The predominantly tropical Acanthaceae comprise some 4000 species in about 230 genera. The family is worldwide in distribution although most genera are restricted to either the New World or the Old World. Mexico is a center of species richness, diversity, and endemism for Acanthaceae. The family is represented there by about 400 species of terrestrial herbs, shrubs, and trees, as well as epiphytes and subaquatics. These occur in a diversity of plant communities at elevations from sea level to 2900 meters. Daniel (1993) summarized information on Mexican Acanthaceae. A more recent estimate of endemism at the rank of species for the family in Mexico is 61% (Daniel 2004a). Mexican Acanthaceae are particularly well represented in the dry forest and scrub communities throughout the country (Daniel 1993). Several regional taxonomic accounts of Mexican Acanthaceae have been published recently (Daniel 1995a, 1997, 1999a; Daniel and Acosta 2003) and a comprehensive treatment of the family for the entire country is being prepared. The following account of Sonoran Acanthaceae was undertaken in response to recent intensive collecting activities in various portions of the state and the need to resolve several taxonomic questions among taxa there.

Physical geography of Sonora.— The state of Sonora in northwestern Mexico is one of that nations largest in area (185,430 square km; second in size after Chihuahua), driest in climate, and least densely populated (García de Miranda and Falcón de Gyves 1986; Stevenson et al. 1988). Most of Sonora lies within the Basin and Range Physiographic Province that consists of broad, alluvial basins at low elevations bordered by long, narrow, and parallel mountain ranges often trending in a northwest to southeast orientation. Eastern Sonora consists of north-south trending mountains forming the western cordillera of the Sierra Madre Occidental, which reaches an elevation of 2625 m at the highest known point in the state (Sierra le los Ajos in northeastern Sonora). The Sonoran climate varies from arid and tropical in the south and west to cool and temperate in the east. The eastern mountains are semiarid and aridity increases northward and westward in the state. Precipitation is bimodal with a monsoonlike summer rainy season (characterized by intense, but often very local, thunderstorms) and winter rains that tend to be gentler in nature, more extensive in coverage, and longer in duration. Summer rains are most pronounced in southern and eastern Sonora and are especially important for species of tropical origin (Felger et al. 2001). Winter rains are best developed toward the northwestern portion of the state. Freezing temperatures in northern and eastern Sonora limit the distributions of many tropical and subtropical species.

Summary of Sonoran Acanthaceae.— The vascular flora of Sonora is estimated to comprise 5000 species (Felger et al. 2001). Among these are 41 species in 15 genera of Acanthaceae: *Anisacanthus* (2), *Aphanosperma* (1), *Blechum* (1), *Carlowrightia* (3), *Dicliptera* (1), *Dyschoriste* (3), *Elytraria* (1), (1), *Holographis* (2), *Justicia* (10), *Odontonema* (1), *Pseuderanthemum* (1), *Ruellia* (7), *Stenandrium* (1), and *Tetramerium* (6). The types (excluding syntypes) of 18 names of Acanthaceae were collected in Sonora. *Justicia* is the most species-rich genus of Mexican Acanthaceae (with more than 100 species in the country; i.e., 25% of the total) and is also the most species rich in Sonora (with 10 species; i.e., 24% of the total). Taxonomic recognition of numerous local and regional endemics has resulted in the proliferation of *Justicia* in Mexico. Among the nine native species of *Justicia* in the state, four are widespread and five are regional endemics. Three species of Acanthaceae that have been collected in Sonora are likely not native to the state: *Justicia spicigera*, *Odontonema cuspidatum*, and *Ruellia malacosperma*. All of these are widely cultivated, have been collected in gardens in the state, and are elsewhere known to either escape from or persist after cultivation.

Sonoran Acanthaceae in a phylogenetic context.— Scotland and Vollesen (2000) presented a comprehensive phylogenetic classification of Acanthaceae based on molecular studies, pollen morphology, corolla aestivation, and other characters. Subsequent studies (e.g., McDade et

al. 2000a) have provided insights into, revisions of, and refinements to this system. Two of the three subfamilies of Acanthaceae treated by Scotland and Vollesen (2000) are present in Sonora: Nelsonioideae (*Elytraria*) and Acanthoideae (all other genera). *Thunbergia* of the subfamily Thunbergioideae is doubtless cultivated in Sonora and *T. alata* Bojer ex Sims might ultimately escape there. Among Acanthoideae, genera representing three major lineages (here treated as tribes) occur in Sonora: Justicieae (*Anisacanthus*, *Aphanosperma*, *Carlowrightia*, *Dicliptera*, *Henrya, Justicia, Odontonema, Pseuderanthemum*, and *Tetramerium*), Acantheae (*Holographis* and *Stenandrium*), and Ruellieae (*Blechum, Dyschoriste*, and *Ruellia*). Among genera of Justicieae several of the lineages delimited by McDade et al. (2000a) are present: New World "justicioid" lineage (*Justicia*), Diclipterinae (*Dicliptera*), *Tetramerium* lineage (*Anisacanthus, Aphanosperma, Carlowrightia, Henrya*, and *Tetramerium*), and *Pseuderanthemum* lineage (*Odontonema* and *Pseuderanthemum*). It is not surprising that several of the rather poorly circumscribed genera of the *Tetramerium* lineage are present in Sonora. This lineage includes numerous genera either restricted to or concentrated in dry regions of Mexico. Of the Acantheae, *Holographis* and *Stenandrium* appear to be particularly closely related to one another; both have the same basic chromosome number ($x = 13$), they are similar palynologically, and there does not appear to be any single macromorphological character that universally distinguishes them (Daniel 1998, 2000). Among Sonoran Ruellieae, *Ruellia* and *Blechum* appear to be more closely related to one another than either is to *Dyschoriste* (Daniel 2000; McDade et al. 2000b).

Palynology.— Pollen of Acanthaceae shows a definite taxonomic (rather than pollinator, ecological, or geographic) basis. As such, it is of considerable utility for characterizing and identifying taxa (e.g., Daniel 1998) and for interpreting phylogeny in the family (e.g., McDade et al. 2000a). Perhaps more so than in some other large families, it is important that pollen of each species of Acanthaceae should be characterized in circumscribing taxa. To this end, and to provide general palynological data for other scientific disciplines (e.g., paleoecology), dry (vs. hydrated) pollen of all Sonoran Acanthaceae was studied to some extent and is illustrated below (Figures 3, 12, 18, 20, 21, 31, 38). Most of the pollen samples for species of Acanthaceae occurring in Sonora were taken from collections from within the state or from nearby regions. Pollen is particularly useful for distinguishing species of *Justicia*, a genus in which there is a diversity of aperture number and accompanying insulae. For example, 2-aperturate (most species), 3-aperturate (*J. longii*), and 4-aperturate (*J. masiaca*) pollen grains are known among Sonoran species of *Justicia* (Figures 20, 21), and the number of rows of insulae bordering the aperture on each side varies from one to three, depending on the species.

Floral phenology.— Flowering periods by month were noted for all species of Sonoran Acanthaceae based on the collections studied for each species. Pooling the known months of flowering for all native Sonoran acanths (Fig. 1) reveals that: 1) during each month of the year at least 12 species have been collected in flower, 2) more species (30) flower in March than in any other month, 3) there are two flowering peaks throughout the year (February–April and September–December), and 4) the fewest species (12) have been collected in flower in June. For the most part, flowering periods of Sonoran Acanthaceae can be correlated with the general bimodal precipitation pattern there. The summer rains of July through September are followed by a dry season that typically gives way to winter rains in December and January (and often into February). A second, and more intense, dry season lasts from March until the onset of summer rains. March is obviously the month during which more species flower, and the period March-April appears to be a major peak for acanth flowering. A second, somewhat smaller, peak in flowering appears to take place beginning in September, culminates in October, and continues into December.

The variation in flowering periodicity among Sonoran Acanthaceae reveals five patterns: 1)

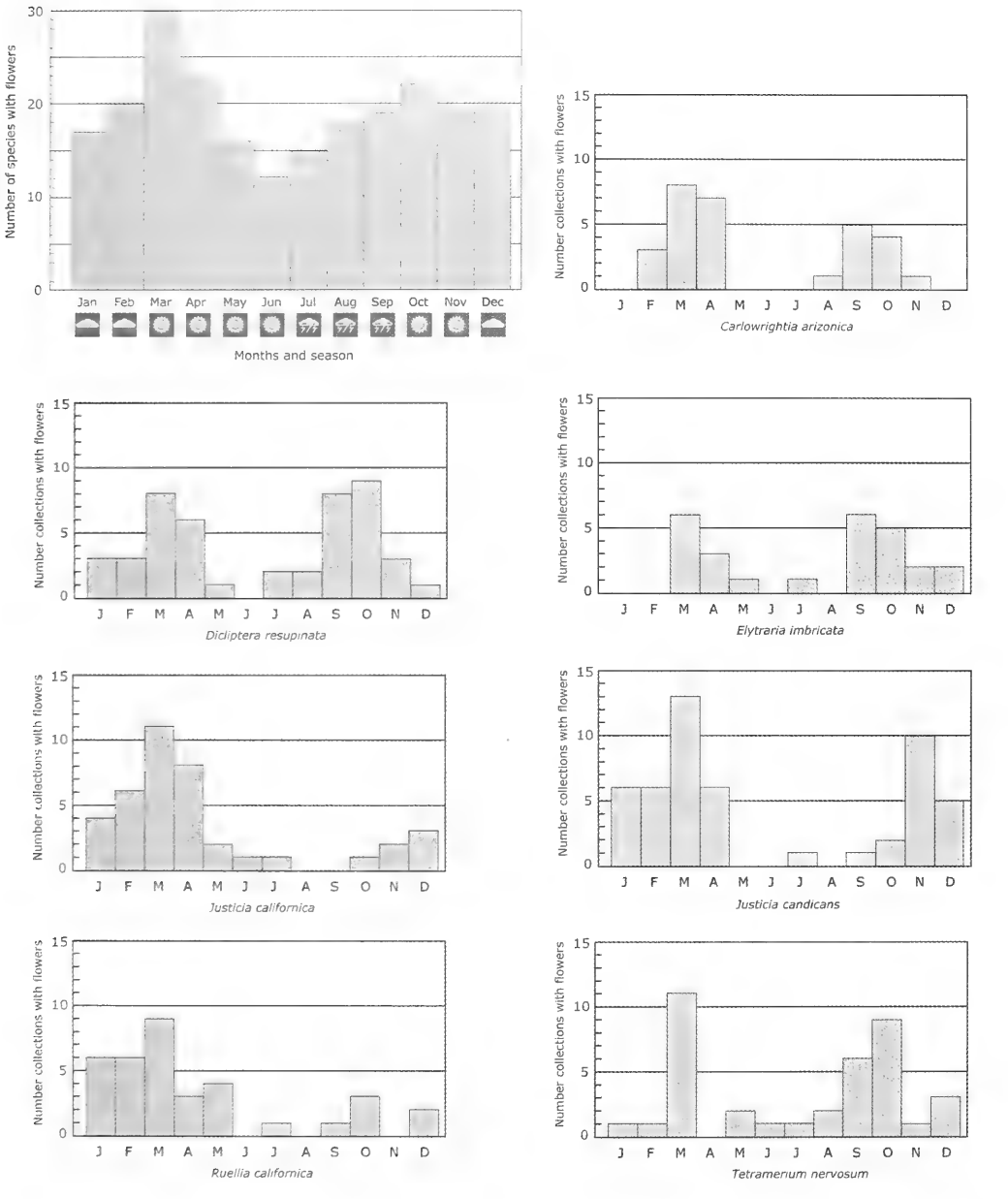


FIGURE 1. Floral phenological data for Sonoran Acanthaceae: histogram at upper left shows the number of species in flower by month; other histograms show peak flowering periods for species with lengthy flowering times based on collections at CAS/DS (see text for additional explanation).

nineteen species flower following both rainy seasons (i.e., *Anisacanthus thurberi, Aphanosperma sinaloensis, Blechum pyramidatum, Carlowrightia arizonica, C. pectinata, Dyschoriste decumbens, D. hirsutissima, Elytraria imbricata, Justicia caudata, J. longii, J. masiaca, J. phlebodes, J. sonorae, Ruellia inundata, R. nudiflora, Tetramerium abditum, T. glandulosum, T. tenuissimum*, and *T. yaquianum*); 2) six species flower only following winter rains (i.e., *Anisacanthus andersonii, Henrya insularis, Holographis pallida, H. virgata, Justicia salviiflora*, and *Stenandrium pilosulum*); 3) two species appear to flower only following summer rains (*Dyschoriste xylopoda* and *Ruellia intermedia*); 4) *Pseuderanthemum praecox* produces chasmogamous flowers following winter rains and cleistogamous flowers following summer rains; and 5) five species have been collected in flower during every month of the year (i.e., *Dicliptera resupinata, Justicia californica, J. candicans, Ruellia californica*, and *Tetramerium nervosum*). Five Sonoran Acanthaceae (*Carlowrightia texana, Justicia hilsenbeckii, Ruellia leucantha, R. parryi*, and *Tetramerium fruticosum*) are each known from the state by a single flowering collection, and thus, there is insufficient data to reveal a pattern for their flowering periods. Based on the date of collection for these species, however, each of them is only known to flower following the period of summer precipitation in Sonora.

It thus appears that most Sonoran Acanthaceae flower immediately following the two rainy seasons, that is, in the first month of each dry season. This is undoubtedly when potential pollinators are most active. Such timing also allows for an extended period of flowering and fruiting prior to the next rainy season when seeds might germinate. Fruit-set is either simultaneous with or begins about a month or two following onset of flowering. Fruits of all Sonoran species mature within a few weeks and expel the seeds. Seeds of 24 species of Sonoran Acanthaceae that have been tested (Daniel unpublished) reveal that no period of dormancy is required prior to germination. Because freezing temperatures are rare in those portions of Sonora where most Acanthaceae occur, sufficient moisture appears to be the primary requirement for germination and establishment in soil. This likely helps to explain the year-round or lengthy flowering periods of some Sonoran Acanthaceae, i.e., they are able to flower opportunistically in response to variable and local rainfall.

In order to determine whether species that have been collected with flowers in most or all months of the year also have one or more peak flowering periods, the number of flowering collections per month was noted for all Sonoran collections at CAS/DS of *Carlowrightia arizonica, Dicliptera resupinata, Elytraria imbricata, Justicia californica, J. candicans, Ruellia californica*, and *Tetramerium nervosum*. These data are summarized in Figure 1. They suggest that *Carlowrightia arizonica, Dicliptera resupinata, Elytraria imbricata, J. candicans*, and *Tetramerium nervosum* are similar to most Sonoran Acanthaceae by having peak flowering periods following both winter and summer rains. All of these species are widely distributed and their flowering throughout (or nearly throughout) the year likely reflects an opportunistic response to adequate precipitation. Both *Justicia californica* and *Ruellia californica* appear to have a peak flowering period only following winter rains. Among the dry regions of Mexico, winter rainfall is largely restricted to the northwestern portion of the country and helps to distinguish the Sonoran Desert from other Mexican deserts. Both *J. californica* and *R. californica* are endemic to northwestern Mexico and nearly restricted to the Sonoran Desert. Their peak flowering periods likely reflect an adaptive response to the winter rains that take place there. Among the six Sonoran Acanthaceae that are only known to flower following winter rains, four of them (*Anisacanthus andersonii, Holographis pallida, H. virgata*, and *Stenandrium pilosulum*) also have distributions restricted to northwestern Mexico.

Major collections of and studies on Sonoran plants.— Because of the state's histori-

cal isolation from major scientific and population centers in the eastern United States and south-central Mexico, botanical explorations in Sonora got a relatively late start. The first comprehensive plant collections, including Acanthaceae, emanating from Sonora resulted from the United States and Mexican boundary surveys following the Treaty of Guadalupe Hidalgo in 1848. Plant collectors attached to the surveying parties included John M. Bigelow, Charles C. Parry, Arthur Schott, E.K. Smith, George Thurber, and Charles Wright. Their Sonoran collections, often accompanied by imprecise locality data, were generally restricted to the northern portions of the state, but included the types of several Acanthaceae. The intrepid Mexican collector Edward Palmer collected in Sonora between 1869 and 1897 and gathered the types of several Sonoran Acanthaceae. During the final two decades of the nineteenth century, Sonora was visited by several prominent plant collectors, all of whom collected Acanthaceae: Townshend S. Brandegee, Marcus E. Jones, Charles R. Orcutt, Cyrus G. Pringle, and Carl A. Purpus. Two botanists, C.A. Hartman and C.E. Lloyd, attached to Carl Lumholtz's expedition to the Sierra Madre Occidental beginning in 1890 collected in northeastern Sonora. Beginning in 1897 and extending through various trips during the first decade of the twientieth century, Joseph N. Rose (often accompanied by others) collected in Sonora (especially in the Pinacate Region, vicinity of Guaymas, and vicinity of Alamos). Collecting activities in the state intensified in the 1930's with the commencement of studies there by Forrest Shreve, Ira Wiggins, and Howard S. Gentry on the vegetation and flora of various portions of the state. Stephen S. White made substantial collections from the region of the Río Bavispe in northeastern Sonora between 1938 and 1941. Following Wiggins's last trip to Sonora in 1962, the major botanical exploration of Sonora was, and continues to be, undertaken by a dedicated group of naturalists from Tucson. Paul Martin, Tom Van Devender, and others have made significant and extensive collections in the nondesert portions of southern Sonora. Richard Felger has made numerous collections in several parts of western Sonora (especially the Gran Desierto, Isla Tiburón and the Seri lands of the adjacent coastal mainland, and in the vicinity of Guaymas). As a result of the activities of these collectors, and given their institutional affiliations or specimen deposition proclivities, the major repositories of Sonoran Acanthaceae are at ARIZ and CAS/DS.

Shreve (1951), Wiggins (1964), Gentry (1942), and White (1948) published pioneering and invaluable studies on plant life in Sonora. These studies were undertaken when significant portions of the state were largely inaccessible. Indeed, some regions of the state remained generally inaccessible until very recently. A cadre of botanists, mostly working from institutions or organizations in Tucson, have recently provided additional, detailed knowledge of vegetation and flora in the state (e.g., Brown 1982; Felger and Moser 1985; Turner et al. 1995; Martin et al. 1998; Felger 2000; Robichaux 1999; Robichaux and Yetman 2000; Felger et al. 2001; Yetman and Van Devender 2002). Most botanical studies in Sonora have concentrated on the Sonoran Desert. Indeed, McLaughlin and Bowers (1999) concluded that the Sonoran Floristic Province (comprising the Sonoran and Mohave deserts) probably has one of the best-known floras, especially for an arid region, of all of the earth's floristic provinces. Recent floristic activities concentrating on the nondesert regions in the vicinities of Alamos and Yécora (e.g., Fishbein et al. 1998; Van Devender et al. 2003) have filled some of the obvious gaps in our knowledge of the state's plant life. Despite the lack of a floristic account of the entire state, as a result of all these studies, Sonora has become one of the botanically best known of Mexico's states. This increased knowledge of Sonora's botanical resources is particularly timely because destruction of natural habitats in the state has accelerated in the past 30 years largely associated with hydrologic modifications and conversion of lowland plant communities to large-scale irrigated agricultural lands.

Phytogeography

Sonora is the meeting ground of three major phytogeographic regions: the Sonoran Floristic Province in the western half of the state, the Madrean Floristic Province in northern and eastern Sonora, and the Central American Floristic Province in central and southern Sonora (*cf.* Takhtajan 1986; McLaughlin and Bowers 1999). Vegetationally, at least 11 regional formations (biomes) in five formation-types (forest, woodland, scrub, grassland, and desertscrub) are represented in the state (Brown and Lowe 1980; Fig. 2). Most prominent among the regional formations are Sonoran desertscrub and thornscrub, which together cover about two-thirds of the state's area and in which more than half of the native species of Sonoran Acanthaceae are found. The following discussion of biotic communities in Sonora is based largely on the excellent summaries found in Brown (1982a), Dimmitt (2000), and Felger et al. (2001). Only the 37 species of Acanthaceae known to be native to Sonora are considered in the context of these communities.

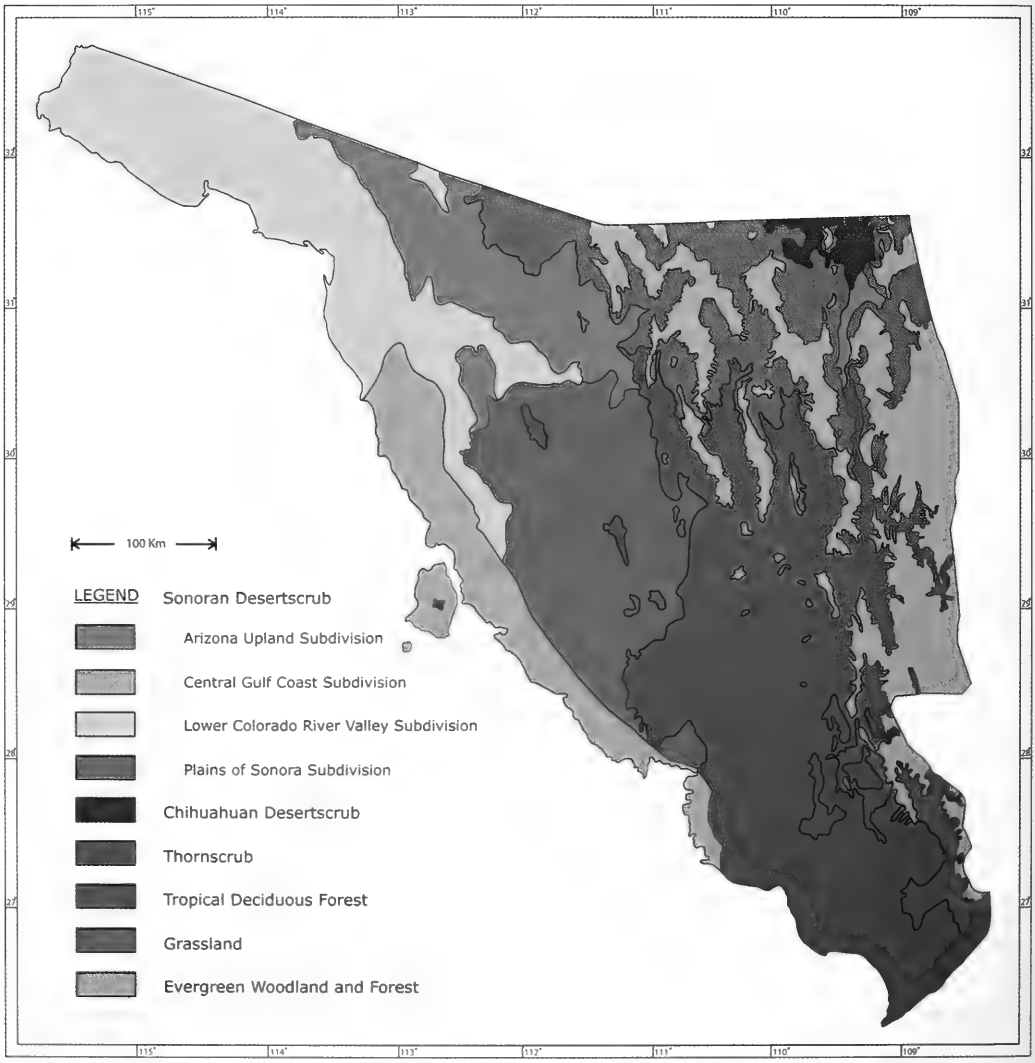


Figure 2. Biotic communities of Sonora modified from Brown and Lowe (1980) and Felger et al. (2001).

Biotic communities of Sonora and Acanthaceae therein.— The western half of Sonora lies within the Sonoran Desert. This large, arid region of northwestern Mexico and the southwestern United States differs from the other three warm deserts of North America (Chihuahuan, Great Basin, and Mohave deserts) by its bimodal rainfall pattern, milder winters, and greater structural complexity of the vegetation. The Sonoran Desert is characterized by open ground with little or no buildup of leaf litter. Its vegetation (Sonoran desertscrub) comprises a great diversity of life forms — especially arboreal elements (trees and columnar cacti), myriad cacti and other succulent plants, and a preponderance of short-lived annuals. In Sonora, the Sonoran Desert is subdivided into four subdivisions: Lower Colorado River Valley, Arizona Upland, Plains of Sonora, and Central Gulf Coast. At least 17 species of Acanthaceae occur in at least one subdivision of the Sonoran Desert. Each subdivision has a distinctive climatic pattern, vegetational physiognomy, and unique assemblage of Acanthaceae.

The Lower Colorado River Valley in northwestern Sonora is the largest, hottest, and driest subdivision of the Sonoran Desert. Vegetation there is open and simple in structure; trees and columnar cacti are absent, rare, or restricted to drainages. Fewer Acanthaceae occur there than in any other subdivision of the Sonoran Desert. The following six species are known from the Lower Colorado River Valley subdivision in Sonora: *Anisacanthus thurberi, Carlowrightia arizonica, Dicliptera resupinata, Holographis virgata, Justicia californica*, and *Ruellia nudiflora*. Among these, most appear to be rare in the subdivision with only *H. virgata* and *J. californica* collected there more than a few times. Included in the Lower Colorado River Valley subdivision is the hyperarid Gran Desierto, near the delta of the Colorado River, in northwesternmost Sonora. Felger (2000) noted only two species of Acanthaceae (*C. arizonica* and *J. californica*) in this region and listed likely limiting factors there as the lack of summer rains and freezing winter temperatures. These two species appear to be the most drought tolerant among Sonoran Acanthaceae, the northern- and western-most occurring acanths in the state, and the only two taxa in the family that occur in the Lower Colorado River Valley subdivision of southern California.

The Arizona Upland in southern Arizona and adjacent Sonora is the highest, wettest, and coldest subdivision in the Sonoran Desert. Trees are common and not restricted to drainages; cacti are common as well. For this subdivision, physiognomy of the vegetation, diversity of life forms, and richness of species are often more suggestive of thornscrub than desertscrub. At least nine species of Acanthaceae occur in the Sonoran portion of the Arizona Upland: *Anisacanthus thurberi, Carlowrightia arizonica, Dicliptera resupinata, Elytraria imbricata, Justicia californica, J. candicans, J. longii, Ruellia nudiflora*, and *Tetramerium nervosum*.

The Plains of Sonora in the west-central portion of the state is the smallest subdivision of the Sonoran Desert and the only one restricted to Sonora. It is similar to the Arizona Upland, but because of warmer winter temperatures and greater precipitation, its vegetation is denser and its flora contains more tropical elements. Its vegetation is dominated by trees, shrubs, and forbs (rather than cacti). At least 14 species of Acanthaceae have been collected there: *Anisacanthus thurberi, Aphanosperma sinaloensis, Carlowrightia arizonica, Dicliptera resupinata, Elytraria imbricata, Holographis virgata, Justicia californica, J. candicans, J. longii, J. sonorae, Ruellia californica, R. intermedia, R. leucantha*, and *R. nudiflora*.

The Sonoran portion of the Central Gulf Coast subdivision consists of a dry, narrow lowland strip along the east coast of the Gulf of California. This region also encompasses Isla San Esteban, Isla Turners, and most of Isla Tiburón in the Gulf of California. Rainfall is meager and sporadic. The vegetation is commonly dominated by stems succulents and generally lacks a low shrub layer. At least 15 Acanthaceae have been collected there: *Anisacanthus thurberi, Aphanosperma sinaloensis, Carlowrightia arizonica, C. pectinata, Dicliptera resupinata, Elytraria imbricata,*

Holographis virgata, Justicia californica, J. candicans, J. longii, J. sonorae, Ruellia californica, R. nudiflora, Tetramerium fruticosum, and *T. nervosum. Tetramerium fruticosum*, a species otherwise restricted to Baja California Sur, has its only known mainland occurrence near Puerto Libertad (see Daniel 1986).

The Chihuahuan Desert occurs primarily on limestone and at generally higher elevations than most of the Sonoran Desert. Unlike Sonoran desertscrub, Chihuahuan desertscrub generally lacks an arboreal element. It consists primarily of grasses, shrubs, and small cacti. In Sonora, Chihuahuan desertscrub is restricted to a small region in the extreme northeastern portion of the state and is surrounded mostly by grassland and oak woodland communities. Five Acanthaceae are known from the limited expanse of Chihuahuan desertscrub in Sonora: *Anisacanthus thurberi, Carlowrightia texana, Dicliptera resupinata, Ruellia nudiflora*, and *R. parryi*. The Sonoran distributions of *C. texana* and *R. parryi* are restricted to Chihuahuan desertscrub, whereas *A. thurberi, D. resupinata*, and *R. nudiflora* occur in other biotic communities in the state. Outside of Sonora, the overall distribution of *R. parryi* is limited to Chihuahuan desertscrub and that of *C. texana* is largely concentrated therein.

Thornscrub is characterized by a generally dense cover of thorny shrubs and small trees that occur in regions with greater precipitation than those covered by desertscrub. In our region it is transitional between the more arid desertscrub and the more mesic tropical deciduous forest between which it is usually positioned in central and southern Sonora. It differs from desertscrub by having denser vegetation with taller trees and cacti and by requiring more moisture. It differs from tropical deciduous forest by its shorter and sparser vegetation that does not require as much moisture. Brown and Lowe (1980) and Brown (1982b) referred to thornscrub in Sonora as "Sinaloan thornscrub." Thornscrub occurs both at low elevations on the coastal plain in southwestern Sonora (coastal thornscrub) and on slopes at somewhat higher (to more than 900 m) elevations, mostly to the east of the Sonoran Desert (foothills thornscrub). Foothills thornscrub was treated by Shreve (1951) as a subdivision of the Sonoran Desert. Label data on herbarium specimens rarely distinguish between coastal and foothills thornscrub. At least 21 species of Acanthaceae are known from thornscrub in Sonora: *Anisacanthus andersonii, A. thurberi, Carlowrightia arizonica, C. pectinata, Dicliptera resupinata, Dyschoriste hirsutissima, Elytraria imbricata, Henrya insularis, Holographis pallida, H. virgata, Justicia californica, J. candicans, J. longii, J. masiaca, J. sonorae, Ruellia californica, R. intermedia, R. nudiflora, Tetramerium nervosum, T. tenuissimum*, and *T. yaquianum*. However, none of them is restricted to this community; most of them also occur in Sonoran desertscrub and or tropical deciduous forest; and some (e.g., *A. andersonii*) occur in regions of thornscrub only along riparian corridors. *Justicia masiaca* is known only from thornscrub and grassland communities.

Tropical deciduous forest (*cf.* "Sinaloan deciduous forest" in Brown and Lowe (1980) and Gentry (1982)) is a wetter, drought-deciduous forest with a conspicuous tropical composition. It is taller and more structurally complex than thornscrub. It generally has a closed canopy 10–15 m above the ground and hosts more vines and epiphytes than other plant communities in Sonora. Tropical deciduous forest is found in southern Sonora between thornscrub at lower elevations to the west and oak woodlands forests at higher elevations to the east. At least 23 species of Acanthaceae occur in Sonora's tropical deciduous forests: *Anisacanthus andersonii, Aphanosperma sinaloensis, Blechum pyramidatum, Carlowrightia arizonica, C. pectinata, Dicliptera resupinata, Dyschoriste hirsutissima, Elytraria imbricata, Henrya insularis, Holographis pallida, Justicia candicans, J. caudata, J. hilsenbeckii, J. phlebodes, J. salviiflora, Ruellia intermedia, R. inundata, R. nudiflora, Tetramerium abditum, T. glandulosum, T. nervosum, T. tenuissimum, T. yaquianum*. Four of them (*B. pyramidatum, J. hilsenbeckii, R. inundata*, and *T.*

glandulosum) are known only from this community in the state. Both *B. pyramidatum* and *R. inundata* are widespread in the Neotropics and occur in diverse communities outside of Sonora. Both species reach the northern extent of their geographic distributions in southern Sonora and their restriction to tropical deciduous forest in the state likely is a result of this being the most tropical of Sonora's biotic communities. Both *J. hilsenbeckii* and *T. glandulosum* are widespread in Mexico, but both are either mostly or entirely restricted to regions of tropical deciduous forest in the country.

In Sonora, grassland communities are mostly found in the northeastern portion of the state at elevations above desertscrub and thornscrub but below woodland and forest communities. Cold-temperate grasslands in Sonora were treated by Brown and Lowe (1980) and Brown (1982c) as "Plains and Great Basin grasslands," two iterations of the North American prairie, with apparently only Plains grassland actually occurring in Sonora. Although various genera of grasses dominate in this community, some trees (largely restricted to riparian corridors) and shrubs are often present. In lower and warmer regions where the presence of trees and shrubs is significant, the resulting grass-shrub community is often referred to as "desert grassland" or "semidesert grassland" (Brown 1982d; McClaran and Van Devender 1995). Desert grassland occupies considerably more area in Sonora than typical Plains grassland. Distinctions between different types of grasslands are rarely indicated on labels of herbarium specimens. Ten species of Acanthaceae (*Anisacanthus thurberi, Dicliptera resupinata, Dyschoriste decumbens, D. hirsutissima, Elytraria imbricata, Justicia californica, J. candicans, J. masiaca, Ruellia nudiflora*, and *Tetramerium nervosum*) are known from grasslands in Sonora, but none of them is restricted to these communities. Based on their mapped distributions and collection data, it would appear that at least *Dyschoriste decumbens* and *Elytraria imbricata* might occur in Plains grasslands. The other Sonoran Acanthaceae that occur in grasslands all appear to have been collected in desert grasslands. Among the five vegetational formation-types in Sonora, grasslands contain the fewest species of Acanthaceae. This would appear to reflect a pattern among all New World Acanthaceae, relatively few of which occur in grasslands.

Several woodland and forest communities dominated by oaks and/or pines occur at elevations above the more arid communities previously discussed. Brown (1982e) and Pase and Brown (1982) referred to them as "Madrean evergreen woodland" and "Madrean montane conifer forest." Ascending in elevation, oak woodlands are usually encountered first. Various species of deciduous and evergreen oaks are found therein. In more mesic sites, the density of oaks may become sufficient to form a closed canopy, resulting in an oak forest. Above the oak zone, oak-pine woodlands and forests occur on the western slope of the Sierra Madre in Sonora. Pines typically form the overstory and oaks the understory in these communities. Pine forests occur at somewhat higher elevations where any of several species of pines become more prominent than the oaks. Oak and pine woodlands and forests are treated together here because information recorded by collectors is often insufficient to distinguish between woodlands and forests and/or between dominance by oaks vs. pines. At least 15 species of Acanthaceae have been collected in oak-pine woodlands and forests of Sonora: *Anisacanthus andersonii, A. thurberi, Dicliptera resupinata, Dyschoriste decumbens, D. hirsutissima, D. xylopoda, Elytraria imbricata, Henrya insularis, Justicia caudata, J. phlebodes, J. salviiflora, Pseuderanthemum praecox, Stenandrium pilosulum, Tetramerium abditum*, and *T. nervosum*. Three of them (*D. xylopoda, P. praecox*, and *S. pilosulum*) are known from Sonora only in these communities. *Stenandrium pilosulum* is restricted to these communities throughout its narrow range, but *P. praecox* and *D. xylopoda* are more widespread and are known from both oak-pine and other biotic communities outside of Sonora. Above the oak-pine zone, a mixed conifer forest occurs in a few high regions in the Sonoran portion of the Sierra Madre Occidental, but Acanthaceae are not known from this community.

New World Acanthaceae are especially abundant in and along watercourses (including ephemeral and perennial streams). Riparian communities in Sonora include: mesquite bosques, palm oases, riparian scrub, and riparian forests. Data on herbarium labels indicate that most (at least 29) species of Sonoran Acanthaceae occur, at least in part, in riparian communities. Riparian corridors often allow intrusions of plants from more mesic communities into the midst of more arid ones, e.g., thornscrub into desertscrub and deciduous forest into thornscrub. This is evident in the distributions of *Aphanosperma sinaloensis* and *Ruellia leucantha*, species of tropical deciduous forests that enter regions of Sonoran desertscrub only along riparian corridors.

Historical phytogeography and current distributional patterns among Sonoran Acanthaceae.— The age and origins of vegetation in Sonora (especially Sonoran desertscrub) have been studied in some detail (e.g., Axelrod 1979; Van Devender 2000) and it is perhaps worthwhile to speculate on the causes of the current distributions of Acanthaceae there. Mexican Acanthaceae are especially abundant in regions of tropical deciduous forest (Daniel 1993). Indeed, this is the most acanth-rich biotic community in Sonora with at least 23 of the 38 presumed native Sonoran Acanthaceae occurring there. In North America, tropical deciduous forests may have had their origins, or at least became increasingly common, in the Eocene (ca. 58 to 36 million years ago) (Van Devender 2000). With the change in climate associated with the rise of the Sierra Madres in southern North America during the Miocene (ca. 24 to 5 million years ago), tropical deciduous forest became restricted to the coastal lowlands in Mexico and thornscrub evolved in drier regions along its margins (possibly including the region now covered with Sonoran desertscrub) (Van Devender 2000). The Sonoran Desert had its origins during a drying trend in the middle Miocene (by about 8 million years ago). Subsequent geologic events that altered both landscapes and climate regimes resulted in contractions and expansions of the Sonoran Desert during the subsequent several millions of years. These perturbations were particularly common during the Pleistocene (beginning 1.8 million years ago) (Van Devender 2000). Sonoran desertscrub was formed by 9000 years ago with relatively modern community composition being achieved about 4500 years ago. Much of the Sonoran Desert's present flora likely predates the Sonoran Desert itself, having evolved in its precursors: seasonally dry thornscrub and tropical deciduous forest. Other plants, primarily those currently restricted to the Sonoran Desert, possibly evolved along with the desert itself. The contractions and expansions of the Sonoran Desert associated with glacial and interglacial cycles likely served as stimuli to both plant speciation and extinction during the Pleistocene.

Although at least 24 species of Sonoran Acanthaceae are found in regions of Sonoran desertscrub and thornscrub, a similar quantity (at least 23 species) is known from the much smaller region of tropical deciduous forest in the state. This reflects both the tropical nature of Acanthaceae and the enrichment of Sonora's flora by the incursions of this biotic community into its southern section. Today, the northern distributional extent of both tropical deciduous forest and thornscrub is in Sonora. This undoubtedly accounts for many of the 22 species of Acanthaceae that attain the northern extent of their distributional ranges in the state. Sonoran Desert is the most "tropical" of the North American warm deserts with its geographic, biologic, and historic connections to these seasonally dry tropical communities. Given these connections to tropical deciduous forest and thornscrub, many primarily Sonoran Desert species reach their southern distributional limits in one of these communities further to the south. Among Sonoran Acanthaceae, *Holographis virgata, Justicia californica, J. longii, J. sonorae, Ruellia californica*, and *Tetramerium fruticosum* appear to have distributions representative of this pattern.

Only one species of Acanthaceae, *Tetramerium yaquianum*, is endemic to Sonora. Fourteen Sonoran Acanthaceae occur only in the state and nearby regions (i.e., southern California, Arizona, New Mexico, trans-Pecos Texas, Chihuahua, Sinaloa, and the peninsula of Baja California), and

can be considered as regional endemics: *Anisacanthus andersonii, A. thurberi, Aphanosperma sinaloensis, Holographis pallida, H. virgata, Justicia californica, J. longii, J. masiaca, J. phlebodes* (also known from Durango), *J. sonorae, Ruellia californica, R. leucantha, Stenandrium pilosulum*, and *Tetramerium fruticosum*. Five of these (*A. andersonii, H. pallida, J. masiaca, J. sonorae*, and *S. pilosulum*) barely occur outside of the state and might be considered as nearly endemic to Sonora. Because the Sonoran Desert is a unique and geographically restricted entity, one might expect considerable endemism associated with it. Indeed, a "greater Sonoran Desert region" (i.e., regions of Sonoran desertscrub and associated thornscrub and desert grassland) harbors at least eight endemic species of Acanthaceae (*Holographis virgata, Justicia californica, J. hians* (Brandegee) Brandegee, *J. longii, J. masiaca, J. sonorae, Ruellia californica*, and *R. comonduensis* T.F. Daniel), with six of them occurring in Sonora.

The overall distributions of 15 Sonoran Acanthaceae are widespread, i.e., they occur in one or several biotic communities over a broad distributional area and they are often weedy: *Carlowrightia arizonica, Blechum pyramidatum, Dicliptera resupinata, Dyschoriste decumbens, D. hirsutissima, Elytraria imbricata, Henrya insularis, Justicia candicans, J. caudata, J. salviiflora, Pseuderanthemum praecox, Ruellia intermedia, R. inundata, R. nudiflora*, and *Tetramerium nervosum*. For example, *Tetramerium nervosum* occurs in numerous communities from the southwestern United States to Peru. The remaining eight species of Sonoran Acanthaceae have overall distributions intermediate between widespread and restricted to northwestern Mexico and the southwestern United States. They are either restricted to a particular biotic community in North America (e.g., *Ruellia parryi* occurs throughout the Chihuahuan Desert in the United States and northern Mexico), or occur in several communities over a somewhat restricted geographic area (e.g., *Carlowrightia texana* occurs in various habitats in the southern United States and northern Mexico). At least two species that occur in regions adjacent to Sonora (and in biotic communities represented in Sonora) might be expected to occur within the state: *Carlowrightia linearifolia* (Torr.) A. Gray and *Ruellia paniculata* L.

Several species of Sonoran Acanthaceae were observed or noted by other collectors to occur in disturbed habitats. These include roadsides, fencerows, ditches, fields, pastures, and recently burned sites. Some, but not all, Acanthaceae occurring in these man-made (or artificially created) habitats are widespread and weedy species (e.g., *Blechum pyramidatum, Elytraria imbricata, Ruellia inundata, Tetramerium nervosum*). As I have noted previously (Daniel 1983a), the propensity of some Acanthaceae to occur in artificially disturbed habitats may reflect a preadaptation among them for occurring in naturally disturbed habitats (e.g., along watercourses). Indeed, as noted above, most Sonoran Acanthaceae have been collected along watercourses of one type or another. Two of these widespread and weedy species have the broadest ecological amplitude among Sonoran Acanthaceae: *E. imbricata* occurs from desertscrub to pine forests (0–1680 m) and *T. nervosum* occurs from desertscrub to oak-pine woodlands (20–1450 m).

The small region supporting Chihuahuan desertscrub in northeasternmost Sonora is one of the least known regions of the state. Recent collecting activity there has resulted in the discovery of two Acanthaceae not previously reported for the state, *Carlowrightia texana* and *Ruellia parryi*. Both of these are common plants that are widespread in the Chihuahuan Desert region of northern Mexico and adjacent portions of the United States. Additional exploration in the region should locate a Sonoran occurrence for *C. linearifolia* (Torr.) A. Gray, another species of the Chihuahuan Desert that occurs in nearby regions of southeastern Arizona and southwestern New Mexico.

Plant/Animal Interactions

Acanthaceae as forage.— Acanthaceae are generally palatable to animals that ingest them. Virtually all Sonoran Acanthaceae serve as browse for both native animals and livestock. Hence, they are often found grazed back to or nearly to the ground; more luxuriant growth is often encountered among cacti and thorny shrubs that make it less accessible to large browsers. Felger (1999) indicated that *Holographis virgata* near Guaymas is heavily browsed by cattle, deer, and rabbits. He also noted (2000:64) that in open places in northwestern Sonora, *Carlowrightia arizonica* "is almost always grazed by rabbits, rodents, and especially chuckwallas, which reduce the plant to a mass of short, stubby stems." Yetman and Van Devender (2002) noted the importance of numerous Acanthaceae as forage for livestock. One of their informants noted that in the tropical deciduous forests of southern Sonora many goats and cows depend on these palatable and abundant plants for survival following the regional rains.

Floral visitors.— Acanthaceae offer two possible rewards for floral visitors and potential pollinators, sugary nectar and protein-rich pollen. Known pollinators of Mexican Acanthaceae include insects, birds, and bats (Daniel 1993). For Acanthaceae that occur in Sonora, the following floral visitors have been noted in Sonora or in nearby regions (based on Daniel 1982, 1983a, 1986, 1990, 1995d; Grant 1983; Hilsenbeck 1990b; Michener 1979; Felger 2000, and unpublished data): thrips (*Justicia californica*), bombyliid flies (*Carlowrightia arizonica, Dicliptera resupinata, Henrya insularis, Tetramerium nervosum, T. tenuissimum*), syrphid flies (*Justicia californica*), apid bees (*Anisacanthus thurberi, Justicia californica, J. candicans*), halictid bees (*Carlowrightia arizonica, Henrya insularis, Justicia californica*), megachilid bees (*Dicliptera resupinata*), xylocopid bees (*Justicia californica, J. candicans*), wasps (*Anisacanthus andersonii, Justicia californica*), butterflies (*Dicliptera resupinata, Henrya insularis, Justicia californica, Tetramerium abditum, T. nervosum*), hawkmoths (*Justicia californica, J. longii*), hummingbirds (*Anisacanthus andersonii, A. thurberi, Justicia californica, J. candicans, Odontonema cuspidatum, Ruellia californica, Tetramerium abditum*), and perching birds (*Justicia californica*). Many of these floral visitors were observed to gather either pollen or nectar; some were nectar robbers only. From these observations, it is evident that a diversity of visitors is attracted to each of several floral forms. For some species, multiple kinds of floral visitors have been implicated as pollinators. For example, both *Anisacanthus thurberi* and *Justicia californica* are effectively pollinated by both hummingbirds and bees. As noted by Michener (1979) this may be a result of having both nectar and pollen as rewards. Based on their floral form and nectar sugar ratios (where determined), probable floral visitors/pollinators for other Sonoran Acanthaceae can be inferred as follows: bees/flies (*Aphanosperma sinaloensis, Carlowrightia pectinata, C. texana, Ruellia* spp., *Tetramerium fruticosum, T. yaquianum*) and butterflies (*Justicia hilsenbeckii, J. masiaca, J. phlebodes, J. sonorae, Pseuderanthemum praecox*). Further documentation of floral visitors, their behaviors, and their effectiveness as pollinators among Acanthaceae is highly desirable.

Ethnobotany of Sonoran Acanthaceae.— Sonora was and is home to several prominent indigenous groups of partially or mostly sedentary farmers: Mayo (southern Sonora), Yaqui (southern Sonora), Pima Alto (northwestern Sonora), Pima Bajo (central and east-central Sonora), Papago or Tohono O'odham (northwestern Sonora), Guarijío (southeastern Sonora), and Opata (central and northeastern Sonora). Historically, the Seri fished, hunted, and gathered wild plants on Isla Tiburón, Isla San Esteban, and along the adjacent coast of the mainland. Ethnobotanical studies published for several of these cultural groups (e.g., Gentry 1963; Felger and Moser 1985; Yetman 2002; Yetman and Van Devender 2002) reveal that each made considerable use the region's plants for a variety of purposes. Uses of and local names given to Acanthaceae by both pre-

Colombian and post-Colombian Americans are cited in this treatment. Some of these are derived from ethnobotanical publications, but many are taken from unpublished information recorded on labels of herbarium specimens.

Materials and Methods

The following taxonomic account of Sonoran Acanthaceae is based on field and herbarium studies over the past 27 years. The generic descriptions are based primarily on New World species. Comprehensive descriptions of species are provided for those not fully and recently described elsewhere or where sufficient additional collections from Sonora have resulted in either taxonomic renovations or significant new morphological information. Otherwise, a reference to a recent description is cited. Complete synonymies are provided for most taxa. For those taxa with many synonyms, only names based on types from Sonora or names applied to Sonoran plants are provided; however in such cases, reference to a recent full synonymy is also cited. The months of flowering and fruiting noted for each species are derived solely from Sonoran collections. Habitat and elevational data are derived primarily from information provided on herbarium specimens. These data have occasionally been augmented based on mapping each collection using the map of biotic communities by Brown and Lowe (1980). Smaller versions of these maps are provided for all Sonoran Acanthaceae that are presumed to be native to the state. Illustrations of macromorphological characteristics are provided for several species and citations of previously published illustrations are also given. This account includes scanning electron micrographs of representative pollen for each species. Discussions deal with morphological variation, nomenclature, and distribution as appropriate for each taxon. All specimens studied are cited.

Taxonomic Treatment

Acanthaceae

Terrestrial (rarely aquatic) perennial herbs or shrubs, less often trees or twining perennial vines, vegetative and floral organs glabrous or pubescent with various types of eglandular (simple and compound), subglandular (i.e., lacking a conspicuous capitate gland at apex but apically enlarged), and glandular trichomes, often covered with cystoliths visible in epidermis (these absent in some genera). Young stems usually with swollen nodes. Leaves opposite and decussate or sometimes quaternate (rarely alternate), simple, estipulate, sessile to petiolate, margin usually entire. Inflorescence of 1–many-flowered dichasia borne in axils of leaves or bracts, dichasia alternate (= solitary) or opposite (= paired) at nodes, sessile or pedunculate, when borne in axils of bracts then usually forming dichasiate spikes (i.e., dichasia and flowers sessile to subsessile), racemes (i.e., dichasia sessile to subsessile and flowers pedicellate), or thyrses (i.e., dichasia pedunculate), if spikes or racemes or thyrses branched then forming panicles. Bracts large and brightly colored or small and green. Flowers sessile or pedicellate, usually subtended by 2 bracteoles, bisexual, chasmogamous and often cleistogamous, rarely heterostylous. Calyx comprising 5 sepals, free or usually fused and deeply 4-5-lobed, lobes equal to unequal in length, sometimes partially or completely fused with one another and forming heteromorphic segments. Corolla sympetalous, comprising 5 petals, tube cylindric or funnelform (i.e., gradually or abruptly expanded distally into a ± distinct throat), sometimes resupinate, limb subactinomorphic or usually bilabiate with an upper lip of 2 lobes and a lower lip of 3 lobes, corolla lobes imbricate (including cochlear and quincuncial) or contorted in bud. Stamens epipetalous, included in corolla tube or exserted from mouth of corolla, usually 2 or 4 and didynamous, anthers 1–2-thecous, sometimes with basal or apical appendages,

thecae of a pair parallel to perpendicular, collaterally attached to filament to superposed to widely separated by a modified connective, pollen extremely diverse, staminodes 0-3. Nectariferous disk usually present around base of ovary, annular. Gynoecium 2-carpellate, ovary superior, generally 2-locular, placentation usually axile, ovules 2-many in each locule, style simple, terminal, filiform, included within corolla tube or exserted from mouth of corolla, stigma funnelform, 2-lobed, or with one lobe suppressed. Fruit a loculicidal, explosively dehiscent, stipitate or estipitate, 2-valved capsule (elsewhere, rarely a fleshy drupe), septa sometimes separating from inner wall of mature capsule. Seeds 2-many, each usually subtended by a prominent hook-shaped retinaculum, globose to lenticular, glabrous or pubescent, trichomes often hygroscopic or becoming mucilaginous when wet. ($x = 7$).

Most of the ca. 4000 species occur in the tropics and subtropics with major centers of endemism, morphological diversity, and species richness in Indo-Malesia, Africa (including Madagascar), South America, and Mexico-Central America. Plants occur in most tropical habitats except those at very high elevations (i.e., above 3000 meters). Sonoran Acanthaceae consist of 41 species in 15 genera.

Key to Genera of Acanthaceae in Sonora

1. Leaves alternate, often crowded at stem apices; inflorescence borne on scapes covered with coriaceous and clasping scales; corollas 4-8.5 mm long; stigma touch-sensitive; capsule 2.8–4.1 mm long; seeds irregularly blocky, borne on papilliform placentae (i.e., hooklike retinacula lacking). . . . . *Elytraria*
1. Leaves opposite, usually ± evenly distributed along stems; inflorescence not borne on scaly scapes; corollas (except in occasional cleistogamous flowers) 5.5–60 mm long; stigma not touch-sensitive; capsule 3.5-30 mm long; seeds subglobose to lenticular, borne on hooklike retinacula.
    2. Fertile stamens 4.
        3. Cystoliths absent; anthers 1-thecous; corolla lobes imbricate (ascending cochlear) in bud; pollen 3-colpate.
            4. Shrubs to 2 m tall; corolla strongly zygomorphic; occurring west of the Sierra Madre Occidental in desertscrub, thornscrub, and tropical deciduous forest at elevations of 20–600 m . . . . . *Holographis*
            4. Acaulescent perennial herbs less than 10 cm tall; corolla appearing subactinomorphic; occurring in the Sierra Madre Occidental of eastern Sonora in oak-pine communities at elevations of 1540–2250 m. . . . . *Stenandrium*
        3. Cystoliths present; anthers 2-thecous; corolla lobes contorted in bud; pollen otherwise.
            5. Inflorescence of densely bracted, often elongate, 4-sided dichasiate spikes with the bracts broadly ovate to cordate to subcircular; placentae separating from mature capsule wall; pollen 3-syncolporate. . . . . *Blechum*
            5. Inflorescence otherwise; placentae remaining attached to mature capsule wall; pollen not 3-syncolporate.
                6. Thecae basally awned or mucronate; calyx tube with weak, usually hyaline, regions proximal to sinuses between lobes; corollas with colored markings within, 13–29 mm long; pollen 3-colporate, mesocolpia multi-striate with 4–15 pseudocolpi. . . . . *Dyschoriste*
                6. Thecae lacking basal awns or mucros; calyx tube lacking weak and hyaline regions proximal to sinuses between lobes; corollas concolorous, 20–65 mm long; pollen 3-porate, exine coarsely reticulate. . . . . *Ruellia*

2. Fertile stamens 2.
   7. Androecium of 2 fertile stamens and 2 staminodes.
      8. Perennial herbs less than 6 dm tall; corolla salverform (i.e., tube cylindric or tapered distally, limb subactinomorphic), the tube 1.5–1.7 mm in diameter at apex, the limb 14–28 mm in diameter, or if chasmogamous flowers absent, then with budlike cleistogamous flowers; calyx 4–6 mm long during anthesis. . . . . *Pseuderanthemum*
      8. Shrubs, often more than 1 m tall; corolla funnelform (i.e., tube gradually expanded distally, limb bilabiate), the tube 2.5–4 mm in diameter at apex, the limb 6.5–13 mm in diameter; calyx 2–4 mm long during anthesis. . . . . *Odontonema*
   7. Androecium of 2 fertile stamens and 0 staminodes.
      9. Stems hexagonal in cross-section; inflorescence of axillary bracteate cymes bearing (1–) 3 (–5) pedunculate cymules; cymules consisting of 1 or more flowers subtended by an involucre of 2 or more pairs of bracteoles; outer pair of cymule bracteoles cordate to deltate, conspicuous and larger than inner pair(s); septa with attached retinacula separating from inner capsule wall at maturity and protruding prominently from each valve of capsule, the mature capsule conspicuously ruptured near base of head; corolla resupinate 180°. . . . . *Dicliptera*
      9. Stems terete to quadrate-alate in cross-section; inflorescence various but not as described above; cymules never present; flowers subtended by 1 pair of bracteoles; retinacula remaining attached to inner capsule wall at maturity or separating slightly near base of head (i.e., *Henrya* and *Tetramerium*) but not protruding prominently from each valve of capsule, mature capsule not or barely ruptured near base of head; corolla not resupinate.
         10. Upper lip of corolla rugulate (i.e., with a stylar furrow); stamens appressed to upper lip of corolla, anthers dehiscing toward lower lip (i.e., flower nototribal); thecae subequally to unequally inserted or superposed, often with a basal appendage on at least one theca; pollen 2 (–3 or 4)-aperturate, apertures al); thecae subequally to unequally inserted or superposed, often with a basal flanked on each side by 1–3 rows of ± circular insulae and/or peninsulae (i.e., al); thecae subequally to unequally inserted or superposed, often with a basal lacking pseudocolpi). . . . . *Justicia*
         10. Upper lip of corolla not rugulate (i.e., lacking a stylar furrow); stamens appressed to lower lip of corolla, anthers dehiscing toward upper lip (i.e., flower stenotribal); thecae equally to subequally inserted, lacking basal appendages; pollen 3-aperturate, apertures flanked on each side by a solid band of exine and a pseudocolpus (i.e., 6-pseudocolpate).
            11. Capsules completely reflexed at maturity, expanded and truncate (to subemarginate) at apex, base of stipe covered with uncinate trichomes; seeds fused to and permanently retained within capsule valves. . *Aphanosperma*
            11. Capsules erect at maturity, narrowed and acute at apex, base of stipe lacking uncinate trichomes; seeds free from capsule valves and ejected therefrom at maturity.
               12. Either bracts or bracteoles conspicuous, concealing calyx; septa with attached retinacula separating slightly from inner wall of mature cap sule near base of head; seeds 0.8–2.8 mm long.
                  13. Bracteoles fused, if at all, only at base for a distance up to 1 mm, not forming an involucre; bracts longer than bracteoles; seeds 4,

lacking trichomes; pollen with colpi narrow, not or barely exceeding width of centrally positioned ora. . . . . *Tetramerium*

13. Bracteoles fused along 1 side from base to near apex, forming a conspicuous involucre; bracts shorter than bracteoles; seeds 2, pubescent with stiff, interwoven, hygroscopic trichomes to 0.5 mm long; pollen with colpi broad, far exceeding width of centrally positioned ora. . . . . *Henrya*

12. Neither bracts nor bracteoles conspicuous, not concealing calyx, or if subfoliose (as in *Anisacanthus thurberi*) then at least calyx plainly visible; septa with attached retinacula remaining attached to inner wall of mature capsule; seeds 2.5–8 mm long.

14. Shrubs to 3 m tall; corollas red to orange, concolorous, (24–) 30–60 mm long; thecae 3–4.8 mm long; capsule 12–30 mm long. . . . . *Anisacanthus*

14. Mostly perennial herbs to 1 m tall; corollas white, cream, or yellow, usually with colored markings, 5.5–18 mm long; thecae 0.5–1.9 mm long; capsule 6.5–14 mm long. . . . . *Carlowrightia*

Anisacanthus Nees

Anisacanthus Nees, Linnaea 16:307. 1842. TYPE: *Anisacanthus quadrifidus* (Vahl) Nees (≡ *Justicia quadrifida* Vahl).

Erect shrubs with cystoliths. Leaves opposite. Inflorescence of dichasia in leaf axils or, more commonly, of dichasiate (spikes to) racemes (to thyrses); dichasia (opposite) alternate, 1 (-3)-flowered, sessile (to pedunculate), subtended by a leaf or a bract. Flowers homostylous, (sessile to) pedicellate, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic, usually accrescent in fruit. Corolla pink, reddish, or orange, lacking colored markings, tube gradually expanded distally, throat indistinct to ± distinct, limb 2-labiate, upper lip comprising 2 fused lobes, entire to emarginate at apex, lower lip 3-lobed with lobes homomorphic and often recoiled, corolla lobes imbricate in bud. Stamens 2, exserted from mouth of corolla, anthers 2-thecous, thecae equal in size, parallel to subsagittate, equally inserted on filament, lacking basal appendages, dehiscing toward upper lip of corolla (i.e., flowers stenotribal); pollen (Fig. 3) euprolate to perprolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed. Capsule stipitate, head subspheric, retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule. Seeds 2–4, homomorphic, lenticular, lacking trichomes. (x = 18).

This American genus of about 18 species has centers of diversity in Mexico (8 species) and Brazil (6 species). Hagen's (1941) revision of the North American species is very much out of date. North American species all occur in arid to semiarid regions. The large, brightly colored, and nectariferous flowers are commonly visited by hummingbirds. In some aspects of floral morphology, the North American species appear more similar to one another than to the Central or South American species. The generic description above is based exclusively on North American taxa.

1. Corolla usually dark red, (38–) 45–60 mm long, lobes of lower lip 20–28 mm long; bracts not subfoliose, 3–6.5 mm long; thecae 3.5–4.8 mm long; capsule 20–30 mm long; style red, 40–65 mm long. . . . . *A. andersonii*

1. Corolla usually orangish, (25-) 30–43 mm long, lobes of lower lip 10–17 mm long; bracts

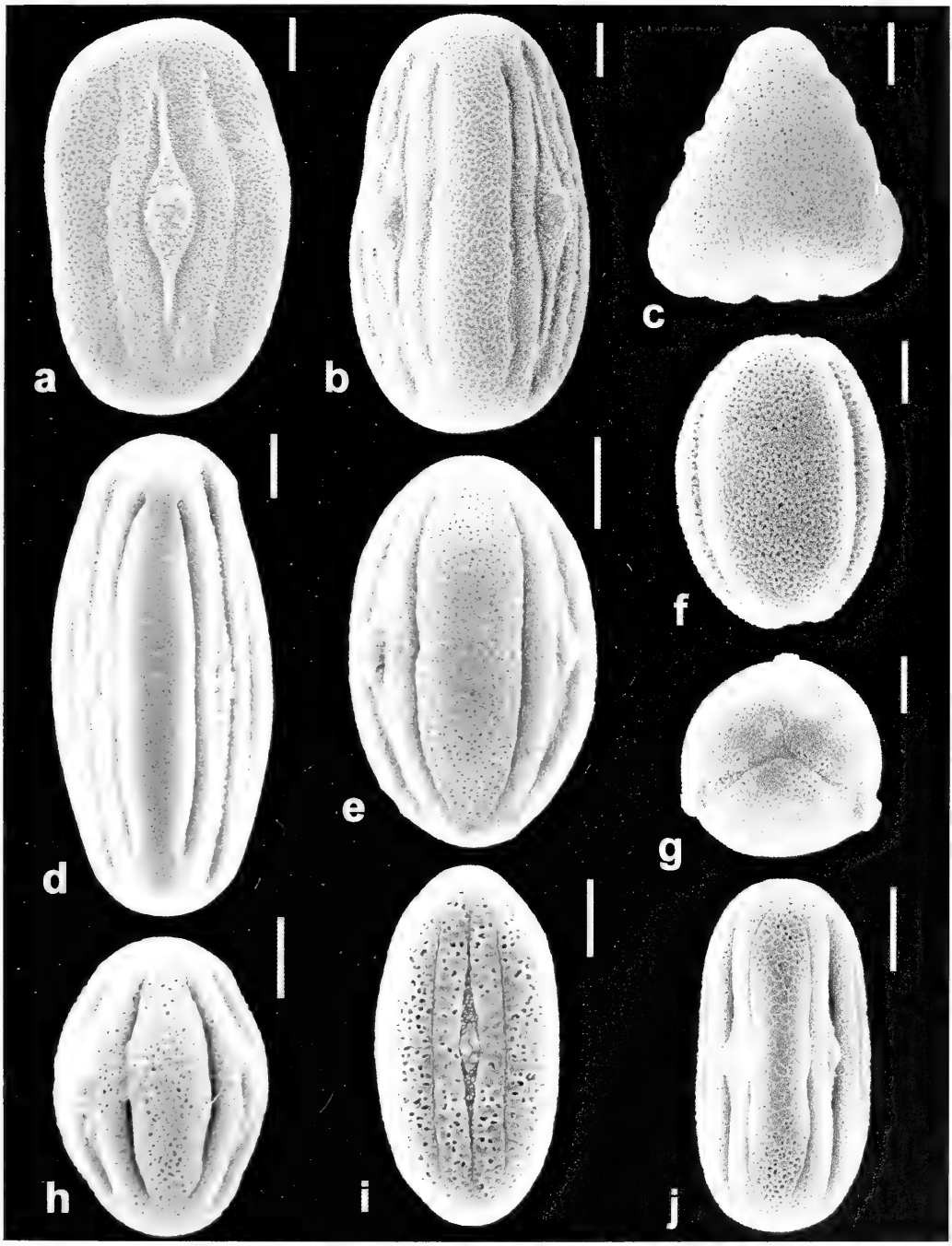


FIGURE 3. Pollen of Sonoran Acanthaceae. a. *Anisacanthus andersonii* (*Gallagher & Hodgson 2814*), apertural view. b. *A. andersonii* (*Gallagher & Hodgson 2814*), interapertural view. c. *A. andersonii* (*Gallagher & Hodgson 2814*), polar view. d. *A. thurberi* (*Daniel 118*), interapertural view. e. *Aphanosperma sinaloensis* (*Van Devender et al. 93-1494*), interapertural view. f. *Blechum pyramidatum* (*Daniel et al. 5454*), interapertural view. g. *B. pyramidatum* (*Daniel et al. 5454*), polar view. h. *Carlowrightia texana* (*Daniel & Butterwick 10000*), interapertural view. i. *C. arizonica* (*Daniel et al. 6845*), apertural view. j. *C. pectinata* (*Daniel et al. 6846*), interapertural view. Scales = 10 μm.

(sometimes caducous) subfoliose, 6.5–28 mm long; thecae 3-4 mm long; capsule 12–17 mm long; style white, 26–44 mm long..... *A. thurberi*

Anisacanthus andersonii T.F. Daniel, Bull. Torrey Bot. Club 109:148. 1982. TYPE: MEXICO. Sonora: Sierra Baviso, Palm Canyon, 17 mi SE of Magdalena on road to Cucurpe (30°28"N, 110°48′W), 1212 m, 19 Mar 1978, *N. McCarten & R. Bittman 2690* (holotype: ARIZ!; isotypes: MICH!, UC!).

Phenology. Flowering: February–July; fruiting: March–July.

Distribution and habitats. Northwestern Mexico (Chihuahua, Sonora); Sonoran plants occur on slopes, in canyon bottoms of riparian gallery forests, and in palm oases in regions of thornscrub, tropical deciduous forests, and oak woodlands at elevations from 480 to 1212 meters.

Illustration. *Bulletin of the Torrey Botanical Club* 109:149. 1982.

Daniel (1982) provided a description of this species. Color of the corolla varies from orange-red to scarlet. Most collections from Sonora have glands inconspicuous or absent in the inflorescence. In *Sanders et al. 4789* (CAS) from Chihuahua, they are conspicuous (to 0.2 mm long) on the rachis, bracts, bracteoles, and calyx. Also, the calyces during anthesis vary from 5-6 mm in length on this collection (vs. 8-12 mm long among other collections of the species). Its identity remains uncertain, and it is not included in the above key. *Breedlove 16445* (CAS, US) from the Sierra Surutato in northern Sinaloa also resembles *A. andersonii*, but it has conspicuous glands (to 0.3 mm long) on these same organs, calyces to 20 mm long during anthesis, and evenly pubescent young stems. It may also represent a different species.

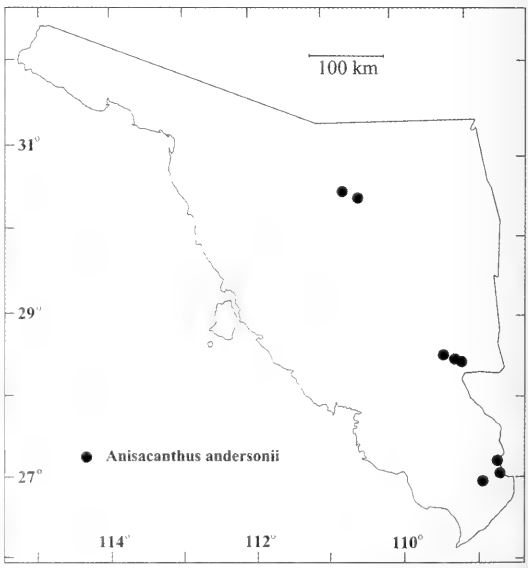


FIGURE 4. Sonoran distribution of *Anisacanthus andersonii*.

Anisacanthus andersonii is endemic to northwestern Mexico. In Sonora, where the species attains the western extent of its geographic range, it is known from canyons or riparian habitats in three isolated regions (Fig. 4). The species tends to occur in somewhat more mesic habitats (and usually at higher elevations) than its close relative, *A. thurberi*. However, *Anisacanthus andersonii* and *A. thurberi* apparently grow in the general vicinity of one another at Ignimbrite Canyon. Martin collected both species there on the same day. Flowers of both are visited by hummingbirds (Daniel 1982) and hybridization between them might occur (see Daniel 1984a). Both species were flowering when collected by Martin, and the distinctions noted in the key above are maintained in his collections.

SONORAN COLLECTIONS: Palm Canyon, 17 mi SE of Magdalena on road to Cucurpe, *R. Bittman 262* (ARIZ); Mpio. Onavas, Rancho La Mula, near Hwy. 16, 18.9 km SE jct. to Onavas, ca. lat. 28°29′N, 109°22′W, *T. Daniel et al. 8553* (ARIZ, ASU, BR, CAS, K, MEXU, MICH, MO, US); Mpio. Yécora, Arroyo La Quema, 0.3 km SE of Tepoca on Hwy. 16, ca. 28°26′N, 109°15′W, *T. Daniel et al. 8634* (CAS); vicinity of 'palm canyon,' 25 km SSE of Magdalena toward Cucurpe, 30°28′N, 110°48′W, *D. Ducote et al. 76-6* (MEXU); Mpio. Magdalena de Kino, 17.4 mi SE of Magdalena on road to Cucurpe, SW part of Sierra Remedio, Palm Canyon, *R. Felger 409* (ARIZ), *3423* (ARIZ, CAS, MEXU); Arroyo Uvalama (Igualamas),

26°59′N, 108°59′W, *M. Fishbein et al. 1104* (ARIZ); ca. 14 mi E of Magdalena, Cañón des Palmas, *P. Gallagher & W. Hodgson 2814* (CAS); Ignimbrite Canyon, 3 km N of La Brisca, Río Santo Domingo, [between Magdalena and Arispe], 30°26′N, 110°33′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); R. San Pedro, 23 km E and 4 km N of Alamos, 27°03′N, 108°42′W, *P. Martin et al. s.n.* (ARIZ); Mpio. Yécora, Arroyo San Nicolás, below San Nicolás, 28°26′N, 109°21′W, *A. Reina G. & T. Van Devender 97-483* (CAS); Mpio. Onavas, Rancho La Mula, 5 km W of Agua Amarilla, 28.2 km E of Río Yaqui on Mex. 16, 28°29′N, 109°22′W, *A. Reina G. et al. 97-116* (ARIZ, CAS, MEXU); Mpio. Yécora, 2.7 km WNW of Tepoca on Mex. 16, 28°28′N, 109°16′W, *A. Reina G. et al. 98-260* (MO); Las Chinacas to Taymucho, *S. Richardson et al. s.n.* (ARIZ); Mpio. Alamos, upper Río Cuchujaqui, 27°06′N, 108°43′W, *R. Rondeau & G. Rodda 90-66* (ARIZ); 17 mi E of Magdalena, Palm Canyon, *R. Thompson & O. Davis 82-40* (ARIZ); Palm Canyon, 17 mi SE of Magdalena in Sierra Babiso (= Cerro Cinta de Plata), *T. Van Devender s.n.* (ENCB); Mpio. Yécora, Arroyo Los Huérigos (tributary of Arroyo San Nicolás) at Mex. 16, 9.3 km E of Tepoca, 3.5 km WNW of San Nicolás, 28°26′N, 109°12′W, *T. Van Devender et al. 96-51* (ARIZ, CAS, MEXU); Palm Canyon in Cerro Cinto de Plata, 17.7 mi SE of Magdalena, *T. Van Devender et al. s.n.* (ARIZ).

Anisacanthus thurberi (Torr.) A. Gray, Syn. Fl. N. Amer. 2(1):328. 1878. *Drejera thurberi* Torr. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):124. 1859. TYPE: UNITED STATES. New Mexico: Las Animas, 1 June 1851, *G. Thurber 352* (lectotype, designated by Rose and Standley, 1912, see discussion below: NY ex Torrey hb.!; isolectotypes: F!, GH! see below).

Shrubs to 1.5 (–3) m tall. Young stems subquadrate, evenly pubescent with an understory of erect subglandular and eglandular trichomes 0.05–0.2 mm long and sometimes with a bifariously disposed overstory of scattered to dense erect to flexuose eglandular trichomes 0.2–1 mm long, soon becoming bifariously pubescent with flexuose to retrorse to retrorsely appressed eglandular trichomes to 1 mm long (hirsute), nodes often hirsute, epidermis of older stems exfoliating in papery strips. Leaves (plants often leafless during anthesis), petiolate, petioles to 7 (–14) mm long, blades narrowly lanceolate to lanceolate to ovate, 11–50 (–65) mm long, (2–) 4–14.5 (–35) mm wide, 3.8–5.6 (–13) times longer than wide, (acute to) acuminate at apex, (rounded to) acute at base, surfaces pubescent with flexuose to antrorse eglandular trichomes to 0.5 mm long. Inflorescence of axillary or terminal dichasiate racemes to 3 cm long, axillary racemes usually borne at nodes of older woody stems and often condensed (i.e., lacking a prominent rachis) and appearing as an axillary cluster of subfoliose bracts and flowers, rachis pubescent like young stems; dichasia 1 (or more)-flowered, opposite, sessile in axils of distal reduced leaves or subfoliose bracts, 1 or more per axil. Bracts sometimes caducous, subfoliose, linear-lanceolate to lance-ovate to elliptic to obovate, (6.5–) 8–28 mm long 1–8.5 mm wide, abaxial surface pubescent like rachis, several pairs of smaller sterile and closely imbricate bracts sometimes present at base of inflorescence. Bracteoles sometimes caducous, linear-lanceolate to linear to linear-elliptic to oblanceolate, (2–) 4–12 (–20) mm long, 0.5–2.5 mm wide, abaxial surface pubescent like bracts. Flowers pedicellate, pedicels 2–10 mm long, pubescent like young stems and also with conspicuous glandular trichomes to 0.3 mm long. Calyx 6.5–14 mm long during anthesis (accrescent and up to 16 mm long in fruit), lobes subulate, 4.5–13 mm long, abaxially pubescent like pedicels. Corolla orange (or sometimes dull reddish), (25–) 30–43 mm long, externally pubescent with erect to flexuose eglandular trichomes 0.1–0.3 mm long, tube (13–) 17–22 mm long, upper lip recurved, strap shaped, 10–22 mm long, entire to 2-lobed at apex, lobes to 0.3 mm long, lower lip 11–21 mm long, lobes often recurved or recoiled, linear, homomorphic, 10–17 mm long. Stamens 19–35 mm long, filaments glabrous, thecae red, 3–4 mm long. Style white, (26–) 28–44 mm long, glabrous, stigma lobes 0.2–0.3 mm long. Capsule 12–17 mm long, glabrous, stipe 5–7 mm long, head 7–11 mm long. Seeds 4.8–7 mm long, 4.4–5.8 mm wide, surfaces smooth to rugose. ($n = 18$).

Phenology. Flowering: October–July; fruiting: October, February–July.

Distribution and habitats. Southwestern United States (Arizona, New Mexico), northwestern Mexico (Sonora); Sonoran plants occur on slopes and along watercourses in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Lower Colorado River Valley, Plains of Sonora), Chihuahuan desertscrub, palm oases, thornscrub, mesquite scrub, mesquite woodlands, desert grasslands, and oak woodlands at elevations from 396 to 1320 m.

Illustrations. Figures 5–6; *Trees, Shrubs and Woody Vines of the Southwest*, 932. 1960; *Trees and Shrubs of the Southwestern Deserts*, 3rd. ed., 217. 1981.

Local names. "Colegaiyo" (Mexican, *Gentry 1309*); "lustieh" (Guarijío, *Gentry 1309*).

The following collections were listed by Torrey in the protologue of *Drejera thurberi* (hence syntypes): "along water-courses, Las Animas, Sonora; June; *Thurber*. Sierra del Pajarito; *Schott*. Cañon of Guadaloupe; April; *Capt. E.K. Smith*." In the Torrey Herbarium at NY, there are several specimens of *A. thurberi*. On one sheet, there are representatives of three collections: a Schott collection from Sonora (now Arizona), "Camp Alamo near Tucson, Sierra del Pajarito," made in July, 1885; a Smith collection from "Cañon of Guadaloupe" (which includes border regions of Sonora, Arizona, and New Mexico); and another Schott collection (no. *732*) from Tucson, Sonora (now Arizona). There are later indications as to which label information goes with which plants on the sheet. There is also a collection of Charles Wright (no. *1456*), collected in 1851–52, which was not mentioned by Torrey in the protologue of *D. thurberi*. Finally, there is the Thurber collection (no. 352, collected in June of 1851) from Las Animas, Sonora (now New Mexico), which was cited in the protologue. *Drejera thurberi* can be assumed to have been lectotypified by Rose and Standley (1912), who noted that the type locality was "along water-courses, Las Animas, Sonora." Johnston (1924) and Standley (1926) also indicated that the type was from Las Animas. Although an herbarium of deposit was neither cited in the protologue nor in any of these indications of the lectotype, and although there are duplicates at other herbaria of Thurber's collection from this locality, the specimen in Torrey's herbarium at NY can considered to be the lectotype (i.e., it is definitely a syntype whereas the duplicates might be isosyntypes). This specimen was annotated by Hagen in 1937 as the type of *A. thurberi* (i.e., of *D. thurberi*), but none of the collections noted by Torrey in the protologue was cited by Hagen (1941). Hagen's annotation does not constitute a typification because it was never published and therefore does not conform to Article 7.10 of the ICBN (Greuter et al. 2000). If the earlier, and likely unintentional, lectotypifications are eventually shown to have been inadequate according to evolving rules on lectotypification in the ICBN (Greuter et al. 2000), then *Thurber 352* at NY is designated here as the lectotype of *Drejera thurberi*. A duplicate of it at F gives a more specific date of collection (1 June 1851).

Most plants of *Anisacanthus thurberi* have orange corollas. Label data of *Reina G. et al. 2004-469* and *Van Devender et al. 89-115* note that the plants collected had red flowers and that the typical orange-flowered plants were present as well. Label data of *Fishbein et al. 2259* also notes variation in flower color from orange to brick-red.

Anisacanthus thurberi occurs in a variety of biotic communities throughout the state (Fig. 7), but appears to be most abundant in Sonoran desertscrub and desert grassland. Although there is some overlap in the habitats of *A. thurberi* and *A. andersonii*, the former tends to occur in more arid situations (and at lower elevations) than the latter. Some ecological aspects of *A. thurberi* were noted by Turner et al. (1995). It reaches the southern extent of its distribution in southern Sonora, where it occurs in thornscrub and possibly in tropical deciduous forest.

Sonoran collections: 10 mi S of Llano, *L. Abrams 13268* (DS); canyon back of Palma, 40 mi S of Hermosillo, *L. Abrams 13349* (DS); 11.2 mi S of cemetery at Agua Prieta, *A. Carter et al. 71-5* (UC); 13 km del Rancho El Colorado, 47 km S de la Garita de Sásabe, *A. Castellanos 192* (MEXU); Palm Canyon, 25 km SSE of Magdalena on road to Cucurpe, 30°28′N, 110°48′W, *D. Ducote 76-6* (MEXU-257162); Rancho La

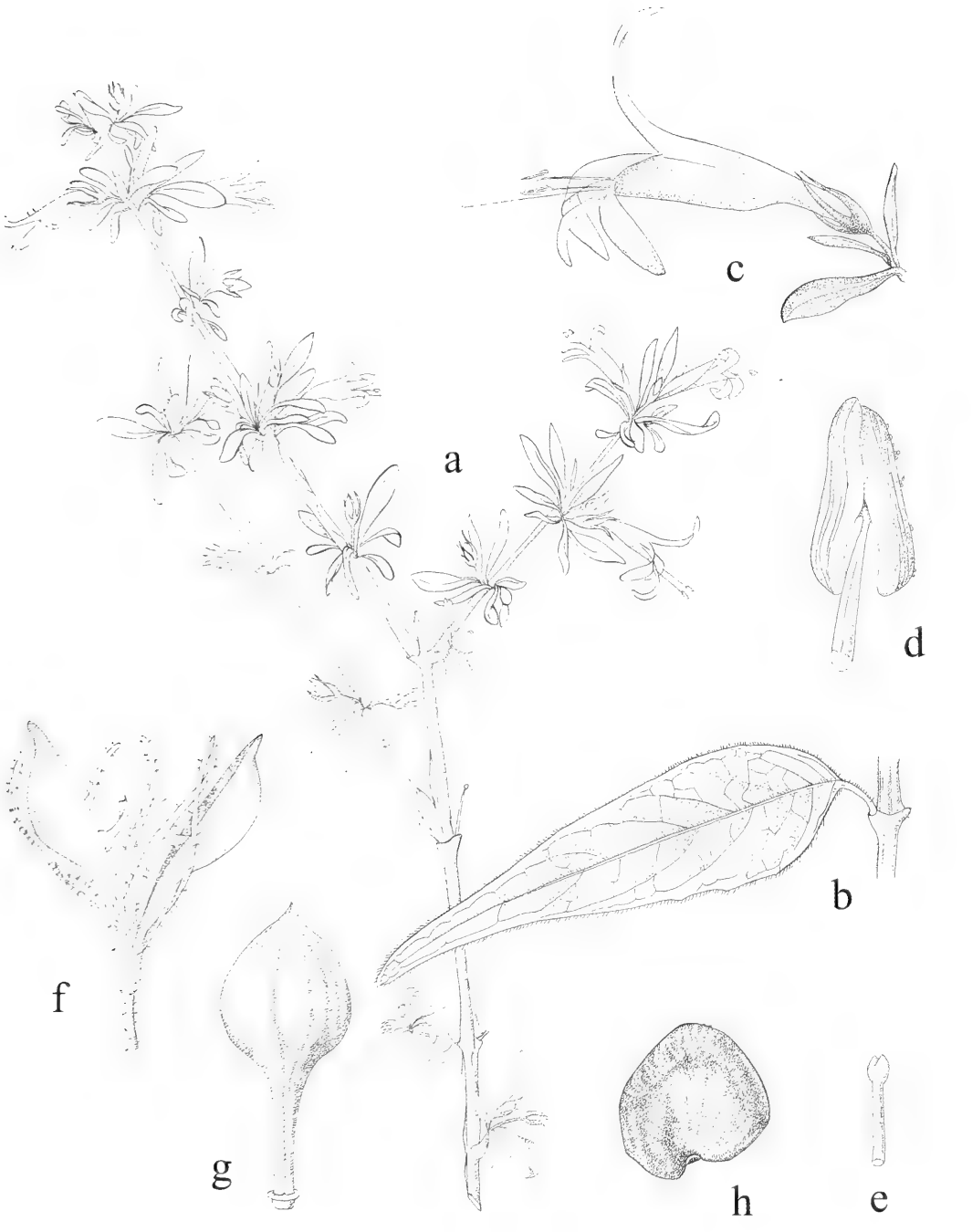


FIGURE 5. *Anisacanthus thurberi*. a. Habit (*Daniel & Butterwick 2911*), × 0.5. b. Vegetative node with leaf (*Daniel 118cv*), × 1.3. c. Inflorescence node with flower (*Daniel & Butterwick 2911*), × 1.5. d. Distal portion of stamen with anther (*Daniel & Butterwick 2911*), × 8.5. e. Distal portion of style with stigma (*Daniel & Butterwick 2911*), × 6.5. f. Dehisced capsule with calyx (*Valenciano s.n.*), × 2.7. g. Undehisced capsule (*Butterwick & Mittleman 8212*), × 2.6. h. Seed (*Butterwick & Mittleman 8212*), × 4.1. Drawn by Zina Deretsky.

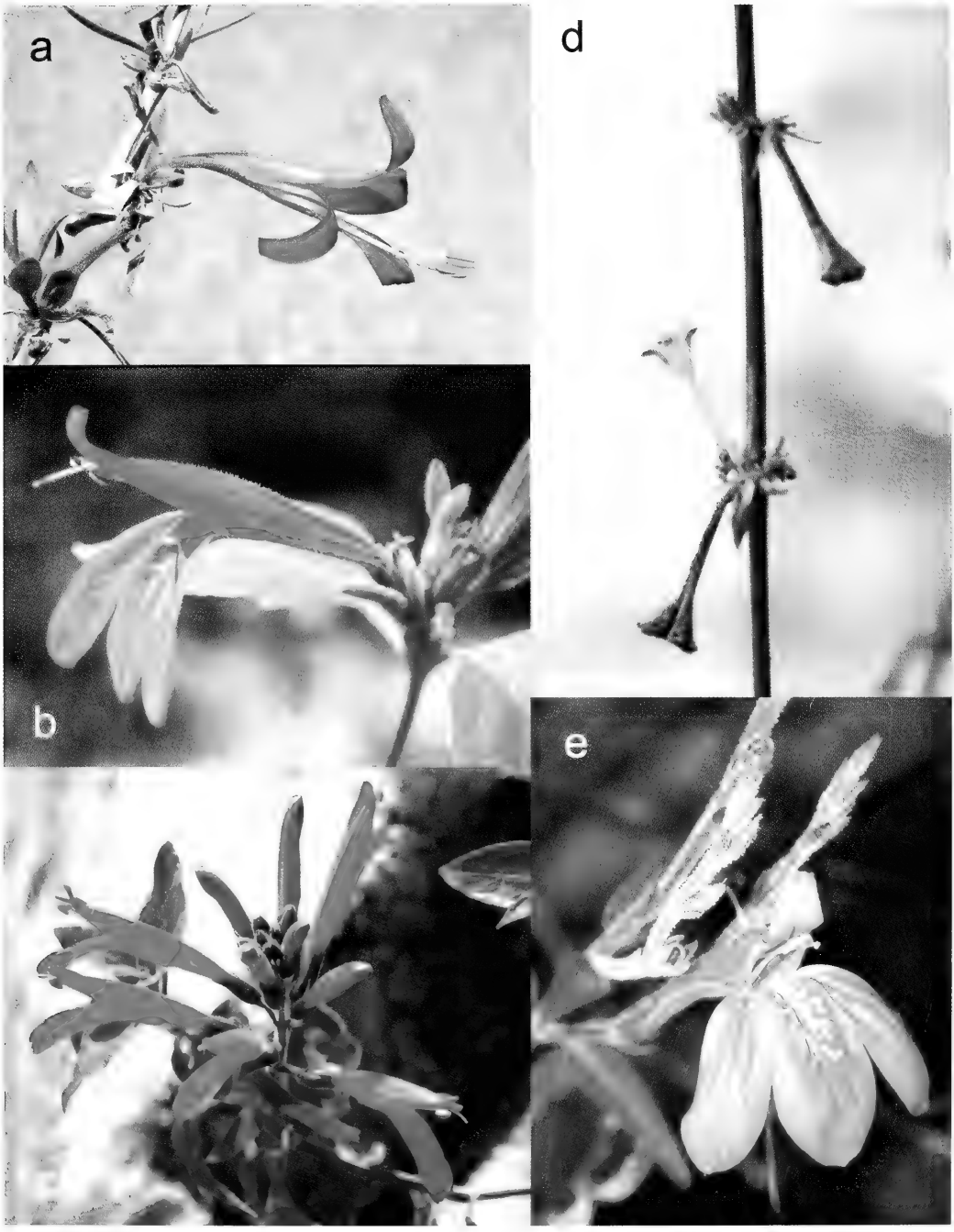


FIGURE 6. Sonoran Acanthaceae. a. *Anisacanthus thurberi*. b. *Justicia candicans*. c. *J. californica*. d. *Aphanosperma sinaloensis*. e. *J. sonorae*.

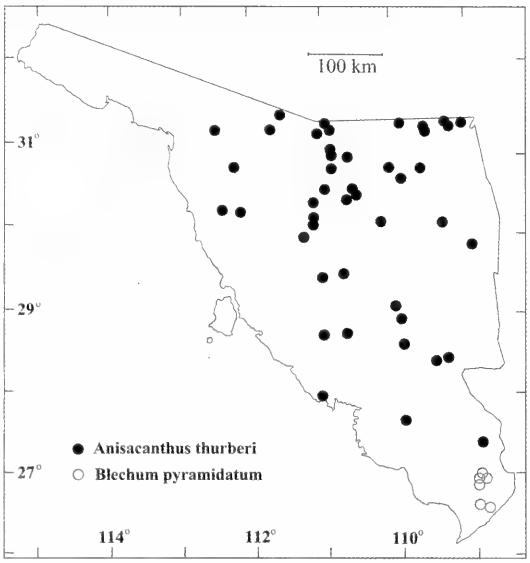


FIGURE 7. Sonoran distributions of *Anisacanthus thurberi* and *Blechum pyramidatum*.

Brisca, ca. 8 mi ENE of Cucurpe, *J. Duek s.n.* (ENCB); Hwy. 83, Nogales, US-Mexico border, *J. Dwyer 14093* (MEXU, MO); San Miguel de Horcasitas, *G. Eisen s.n.* (UC); 4 mi E of Rancho La Primavera in western foothills of Cerro Jojoba, S of Caborca, *R. Felger & H. Gentry s.n.* (ARIZ); Mpio. Imuris, 14.7 mi N of Imuris on Mex. 15, *R. Felger & J. Wright 7266* (ARIZ, CAS, MEXU); ca. 0.5 mi from San Carlos Bay, ca. 8 mi N of Guaymas, *R. Ferris 8736* (DS, US); 9 mi from Imuris in canyon of Magdalena River, *R. Ferris 8799* (DS); Sierra de Los Ajos, 3 mi SE of Mututucachi, 10.4 mi SW of Rancho La Volanta, 30°44′N, 109°59′W, *M. Fishbein et al. 2259* (ARIZ, MEXU); 277 km S of Nogales on road to Hermosillo, *T. Frye & E. Frye 2284* (DS, GH, NY, UC, US); San Bernardo, Río Mayo, *H. Gentry 1309* (A, ARIZ, F, MEXU, MO, NY, S, UC, US, WIS); 13 mi SE of Bacoachi along road to Nacozari, *H. Gentry & Arguelles 22930* (ARIZ, MEXU, US); 100 mi S of Nogales along Mex. 15, *D. Goldberg & T. Van Devender 76-2* (ARIZ); Oputo, *C. Hartman 194* (GH); Nacori, *C. Hartman 277* (GH, PH, US); 2 mi N of San Carlos Bay, *P. Hutchison 2448* (MEXU, UC, US); San Carlos Bay, *I. Johnston 4360* (CAS, GH, US); Mpio. Yécora, Rancho El Palmar, 20 km E of Onavas, 28°29-30′N, 109°23′W, *E. Joyal 1957* (CAS, MEXU, TEX), *2055* (CAS); 5 mi NW of Caborca on road to Tajitos, *D. Keck 4053* (C, CAS, DS, MO); between Caborca and Quitovac, 18 mi NW of Tajitos, near Garambullo, *D. Keck 4110* (DS); El Alamo near Magdalena, *P. Kennedy 7107* (CAS, UC, US); 15 mi SE of Cucurpe, *R. Marin MF65-34* (ENCB); Ignimbrite Canyon, La Brisca, Río Santo Domingo, 30°26′N, 110°33′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); Cajón Bonito [vic. of Agua Prieta], *R. McManus & C. Mason 728* (ARIZ); Mexican line S of Bisbee, Arizona, *E. Mearns 1024* (DS), *1031* (DS); Torres, *C. Purpus 409* (MO, UC, US); Mpio. Imuris, 2.7 km S of Imuris on Mex. 15, 30°45′N, 110°51′W, *A. Reina G. & T. Van Devender 98-496* (CAS, MEXU, TEX); Mpio. Nogales, SE edge of Nogales on road to Santa Cruz, 31°18′N, 110°54′W, *A. Reina G. & T. Van Devender 2001-528* (CAS, MEXU); Mpio. Altar, 4.8 km W of Las Ladrilleras (6.6 km S of Sásabe on road to Altar) on road to Chula Vista, 31°26′N, 111°36′W, *A. Reina G. et al. 2003-1297* (CAS); Mpio. Nogales, 16 km W of Mex. 15 on roqad to Sáric, SW of Nogales, 31°07′N, 111°04′W, *A. Reina G. et al. 2004-188* (CAS); Mpio. Villa Pesqueira, 10.9 km NE of Mátape (Villa Pesqueira) on road from San Pedro de la Cueva to Mazatan, 29°11′N, 109°56′W, *A. Reina G. et al. 2004-469* (CAS); ca. 8 km E of Tecoripa on Hwy. 16, Rancho San Juanico, *R. Rondeau 89-82* (ARIZ, CAS); 23 mi S of Santa Ana along Hwy. 15 (ca. 30°14′N, 111°06′W), *A. Sanders et al. 2469* (TEX); 30 mi NW of Hermosillo, *F. Shreve 5981* (ARIZ, F); 20 mi W of Estación Noria, *F. Shreve 6055* (ARIZ, F); San Carlos Bay, ca. 15 mi NW of Guaymas, *F. Shreve 6553* (ARIZ), *7304* (ARIZ); 5 mi NW of Caborca, *F. Shreve 7529* (ARIZ); Cañón of Guadaloupe, *E. Smith s.n.* (NY); Mpio. Imuris, microondas 14 km S de Imuris, 30°52′N, 110°50′W, *P. Tenorio L. & C. Romero de T. 13517* (CAS, IEB, MEXU, TEX, WIS); Mpio. Agua Prieta, 67 km E de Agua Prieta, carr. a Janos, 31°19′N, 109°18′W, *P. Tenorio L. & C. Romero de T. 13651* (CAS, IEB, MEXU, WIS); Hermosillo to Sahuaripa road, ca. 70 mi E of Hermosillo, *L. Toolin & K. Roever 584* (ARIZ); 11.2 mi S of cemetery at Agua Prieta, 31.2°N, 109.6° W, *R. Turner et al. 71-5* (ARIZ); 9.3 km S de Cíbuta por Mex. 15, ca. 35 km S de Nogales, 30°59′N, 110°52′W, *T. Van Devender 95-549* (ARIZ); Rancho Seri, 5.3 mi S of Rancho el Carrizo (which is ca. 11 mi S of Benjamín Hill and 14 mi W of Mex. Hwy. 15, *T. Van Devender et al. 89-115* (ARIZ); Mpio. Yécora, just NW of Curea, 28°18'40"N, 109°16'40"W, *T. Van Devender et al. 99-136* (ARIZ, CAS, MEXU); 25 mi N of Puerto Libertad, 30°10′N, 112°25′W, *G. Webster 22487* (ARIZ, DAV, MEXU, TEX); 7 mi S of Onavas, 23.5 mi S of Tónichi, 28°23′N, 109°33′W, *G. Webster 23821* (DAV, MEXU); Cañada Motepori, ca. 9 mi NW of Banámichi crossing, ca. 30°04′N, 110°20′W, *G.*

Webster & R. Murphey 21476 (ARIZ, DAV); 20 mi W of Norio, *I. Wiggins 6172* (DS, US); Río Magdalena at Imuris, *I. Wiggins 6198* (DS); 17 mi NE of Cajeme on road to Tesopaco, *I. Wiggins 6396* (DS, UC, US); 5.7 mi NW of Caborca toward Sonoyta, *I. Wiggins 8255* (DS, UC); 24 mi E of Imuris, *I. Wiggins 11676* (DS, TEX, UC, US); 4.6 mi E of Rancho Mababi, *I. Wiggins 11753* (DS, TEX, US).

Aphanosperma T.F. Daniel

Aphanosperma T.F. Daniel, Amer. J. Bot. 75:547. 1988. TYPE: *Aphanosperma sinaloensis* (Leonard & Gentry) T.F. Daniel (≡ *Carlowrightia sinaloensis* Leonard & Gentry).

Erect perennial herbs to shrubs with cystoliths. Leaves opposite. Inflorescence of dichasiate spikes; dichasia (alternate to) opposite, 1-flowered, sessile, subtended by a bract. Flowers homostylous, sessile to subsessile, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes equal to subequal in size. Corolla cream to white with purple markings on upper lip, tube subcylindric, throat indistinct, limb 2-labiate (although sometimes appearing nearly regular), upper lip comprising 2 fused lobes, emarginate at apex, lower lip 3-lobed, corolla lobes imbricate in bud. Stamens 2, exserted from mouth of corolla, anthers 2-thecous, thecae equal in size, subsagittate to subparallel, equally to subequally inserted on filament, lacking basal appendages, dehiscing toward upper lip of corolla (i.e., flower stenotribal); pollen (Fig. 3) euprolate to perprolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, poles sometimes with a 3-armed aperturelike indentation, arms aligned with colpi and extending from pole toward equator, exine reticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed. Capsule stipitate, cuneiform, reflexed at maturity, stipe densely pubescent at base with uncinate trichomes, head truncate to ± emarginate at apex, retinacula not visible in mature capsule. Seeds 2, permanently invested in capsule valves. ($x = 18$).

The genus consists of a single species from tropical dry forests in northwestern Mexico.

Aphanosperma sinaloensis (Leonard & Gentry) T.F. Daniel, Amer. J. Bot. 75:548. 1988. *Carlowrightia sinaloensis* Leonard & Gentry, Brittonia 6:327. 1948. TYPE: MEXICO. Sinaloa: Cerro Prieto, vicinity of Culiacán, 30 Nov 1944, *H. Gentry 7111* (holotype: US!; isotypes: ARIZ!, CAS!, DS!, F!, GH!, MICH!, NY!, PH!, RSA!, UC!).

Phenology. Flowering: October–March; fruiting: October–March.

Distribution and habitats. Northwestern Mexico (Baja California Sur, Sinaloa, Sonora); Sonoran plants occur on slopes, along watercourses, and in canyon bottoms in riparian Sonoran desertscrub (Central Gulf Coast, Plains of Sonora) and tropical deciduous forests at elevations from 60 to 740 m.

Illustrations. Figure 6; *American Journal of Botany* 75:548. 1988; *Proceedings of the California Academy of Sciences* 49:319. 1997.

Descriptions of *Aphanosperma sinaloensis* were provided by Daniel (1988a, 1997). This unispecific genus is endemic to northwestern Mexico and is known primarily from Sonoran collections (Fig. 8). It attains the northern extent of its distribution in west-central Sonora. Although its distribution includes regions of Sonoran Desert, all such occurrences appear to be in thornscrub or deciduous forests that intrude into regions of desertscrub along watercourses. Flowers of *A. sinaloensis* are similar to those of *Carlowrightia pectinata* and *C. arizonica*, but its capsules are unique among Mexican Acanthaceae in four features: they are apically truncate, they reflex as they mature, they have uncinate trichomes at the base, and their seeds are permanently retained. Specimens from Sonora resemble the type and other collections from Sinaloa. Plants from these

two states of mainland Mexico differ from those occurring in the Cape Region of Baja California Sur by their larger corollas (7–10 vs. 5.5–6.8 mm long), longer stamens 4.5–6.5 vs. 3.7–4.3 mm long), and pollen without (vs. with) a polar aperture (Daniel 1997).

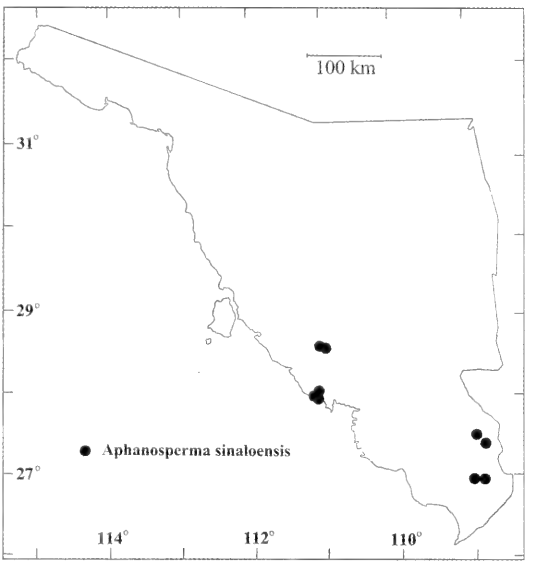


FIGURE 8. Sonoran distribution of *Aphanosperma sinaloensis*.

SONORAN COLLECTIONS: N end of Sierra Libre, mouth of Cañada Prieta, 28°35′N, 110°58′W, *T. Burgess et al. 6747* (CAS); La Pintada, 49 km S de Hermosillo, carr. 15, 28°35′N, 110°58′W, *A. Búrquez & R. Felger 93-22* (MEXU); Cañón Nacapules, ca. 4 km N of Bahía San Carlos, *R. Felger & B. Straub 85-1316* (CAS, MEXU, TEX); Mpio. Guaymas, Cañón del Nacapule, 6 km N of San Carlos Road, 28°01′N, 111°02′W, *R. Felger & F. Reichenbacher 85-1221* (ARIZ, CAS, MEXU, MO, TEX); Cañón las Barajitas, Sierra el Aguaje, ca. 18 km NW of San Carlos, ca. 28°03-04′N, 111°11-12′W, *R. Felger & M. Wilson 95-133* (ARIZ, CAS, MEXU), *95-198* (ARIZ, CAS); Mpio. Guaymas, N side of Sierra el Aguaje, Arroyo Las Pirinolas, ca. 5.6 km S from Rancho Las Pirinolas, 28°03′N, 111°03′W, *R. Felger et al. 02-246* (CAS); Río Mayo region, Arroyo Gochico, ca. 4.5 km E of San Bernardo, 27°24′N, 108°47′W, *M. Fishbein et al. 2138* (ARIZ, CAS, MEXU); Distr. Alamos, Arroyo Cuchuhacki [Cuchujaqui]. *H. Gentry 854* (DS, F, MICH); Mpio. Alamos, Sierra de Alamos along Arroyo El Huirotal, ca. 26°57′N, 108°57′W. *V. Steinmann 1290* (ARIZ, CAS, NY); Río Mayo region, near Tojibampo, 19.5 km NNW of San Bernardo on road to Mesa Colorada, 27°02′N, 108°47′W, *T. Van Devender et al. 93-1494* (ARIZ, CAS, MO, TEX).

Blechum P. Brown

Blechum P. Browne, Civ. Nat. Hist. Jamaica 261. 1756. TYPE: *Blechum brownei* Juss. (≡ *Ruellia blechum* L.; = *Blechum pyramidatum* (Lam.) Urb.).

Spreading to decumbent to erect perennial herbs or shrubs with cystoliths. Leaves opposite. Inflorescence of mostly terminal densely bracteate dichasiate spikes; dichasia opposite, 1-3-flowered, sessile to subsessile (i.e., peduncles to 1 mm long), subtended by a bract (or sometimes a distal leaf). Flowers homostylous, sessile, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic or subequal in length. Corolla white to blue to purplish, tube expanded distally into a distinct throat, limb subregular and ± equally 5-lobed to subbilabiate with upper lip 2-lobed and lower lip 3-lobed, corolla lobes contorted in bud. Stamens 4, didynamous, included in corolla tube or barely exserted from mouth of corolla, anthers 2-thecous, thecae equal in size, parallel, equally inserted on filament, lacking basal appendages, dehiscing toward lower lip of corolla (i.e., flower nototribal); pollen (Fig. 3) oblate spheroidal to euprolate, 3-syncolporate, exine finely to coarsely reticulate; staminodes 0. Style included in corolla tube, stigma 2-lobed or with only 1 lobe prominent or evident. Capsule substipitate, ellipsoid, retinacula present, septa with attached retinacula separating from inner wall of mature capsule. Seeds 8-12, homomorphic, lenticular, beset with hygroscopic trichomes on and near margin. ($x = 17$).

This genus of fewer than 10 species is native to tropical America. *Blechum pyramidatum*, a weedy species, has become naturalized in the Paleotropics.

Blechum pyramidatum (Lam.) Urb., Fedde Repert. Spec. Nov. Regni. Veg. 15:323. 1918. *Barleria pyramidata* Lam., Encycl. 1:380. 1785. TYPE: SANTO DOMINGO. An illustration of Plumier (Pl. Amer. 2:t. 42, fig. 3. 1756) was cited; specimens, if any exist, not seen.

Ruellia blechum L., Syst. Nat., ed. 10, 2:1120. 1759, as "blechnŭ". *Blechum brownei* Juss., Ann. Mus. Natl. Hist. Nat. 9:270. 1807. *Blechum blechum* (L.) Millsp., Publ. Field Columbian Mus., Bot. Ser. 2:100. 1900. TYPE: illustrations of Sloane (Voy. Jamaica 1:t. 109, fig. 1. 1707) and Plumier (Pl. Amer. 2:t. 42, fig. 3. 1756) were cited (syntypes); see Proc. Calif. Acad. Sci. 48:255. 1995.

Phenology. Flowering: March–July, October–November; fruiting: February–July, October–November.

Distribution and habitats. Southern United States (Florida), Mexico (Baja California Sur, Campeche, Chiapas, Colima, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Veracruz, Yucatán), Guatemala, Belize, Honduras, El Salvador, Nicaragua, Costa Rica, Panama, West Indies, Colombia, Venezuela, Guyana, Suriname, French Guiana, Peru, Bolivia, Old World tropics (where presumably introduced); Sonoran plants occur along watercourses and in disturbed areas in regions of tropical deciduous forest at elevations from 150 to 400 m.

Illustrations. Figure 9; *Fieldiana, Botany* 24(10):343. 1974; *Flora of the Bahama Archipelago*, 1346. 1982; *Flora of the Venezuelan Guayana*, vol. 2, 344. 1995; *Flora of Chiapas* 4:17. 1995; *Flora del Valle de Tehuacán-Cuicatlán* 23:14. 1999; *Flora del Bajio* 117:13. 2003.

Daniel (1995a, 1999a) and Daniel and Acosta (2003) provided descriptions of this widespread and weedy species. Use of the name *B. pyramidatum* versus *B. brownei* was discussed by Daniel (1995b). *Blechum pyramidatum* reaches the northern extent of its distribution in southern Sonora (Fig. 7). Sonoran collections greatly resemble plants described from other regions of Mexico and cleistogamous flowers are sometimes evident among them.

Sonoran collections: southeastern border of Alamos (road to mirador), ca. lat. 27°01′N, long. 108°56′W, *T. Daniel 9769* (CAS); Güirocoba crossing of Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56′N, 108°53′W, *T. Van Devender 92-514* (ARIZ); Río Cuchujaqui, Rancho el Conejo, 13.4 km SSE of Alamos, 26°54′N, 108°55′W, *T. Van Devender 92-621* (ARIZ); Alamos, 27°01′N, 108°50′W, *T. Van Devender 94-204* (ARIZ); El Ranchería crossing of Río Cuchujaqui, ca. 22.5 km S of Alamos on road to El Chinal, 26°51′N, 108°55′W, *T. Van Devender & S. Friedman 92-692* (ARIZ, CAS); Río Cuchujaqui near jct. of Arroyo El Mentidero, 11 km S of Alamos, 26°55′N, 108°55′W, *T. Van Devender et al. 92-212* (ARIZ, CAS); Arroyo Alamos between jcts. with Arroyo Potrero and Río Cuchujaqui, 9 km SE of Alamos, 26°58′N, 108°52′W, *T. Van Devender et al. 93-1427* (ARIZ); Río Cuchujaqui, ca. 1 km SW of Los Muertos, 26°44′N, 108°55′W, *T. Van Devender et al. 94-903* (ARIZ); Río Cuchujaqui at El Paso, 26°41′N, 108°49′W, *T. Van Devender et al. 95-87* (ARIZ); Alamos, 27°01′N, 108°50′W, *T. Van Devender et al. 2000-13* (MEXU).

Carlowrightia A. Gray

Carlowrightia A. Gray, Proc. Amer. Acad. Arts 13:364. 1878, nom. cons. LECTOTYPE (Bremekamp, Ind. Nom. Gener. Card 01197. 1956): *Carlowrightia linearifolia* (Torr.) A. Gray (≡ *Schaueria linearifolia* Torr.).

Cardiacanthus Nees & S. Schauer in A. de Candolle, Prodr. 11:331. 1847, nom. rej. TYPE: *Cardiacanthus neesianus* S. Schauer ex Nees. (≡ *Carlowrightia neesiana* (S. Schauer ex Nees) T.F. Daniel).

Croftia Small, Fl. S.E. U.S. 1088. 1903, non King & Prain (1896). TYPE: *Croftia parvifolia* (Torr.) Small (≡ *Schaueria parvifolia* Torr.).

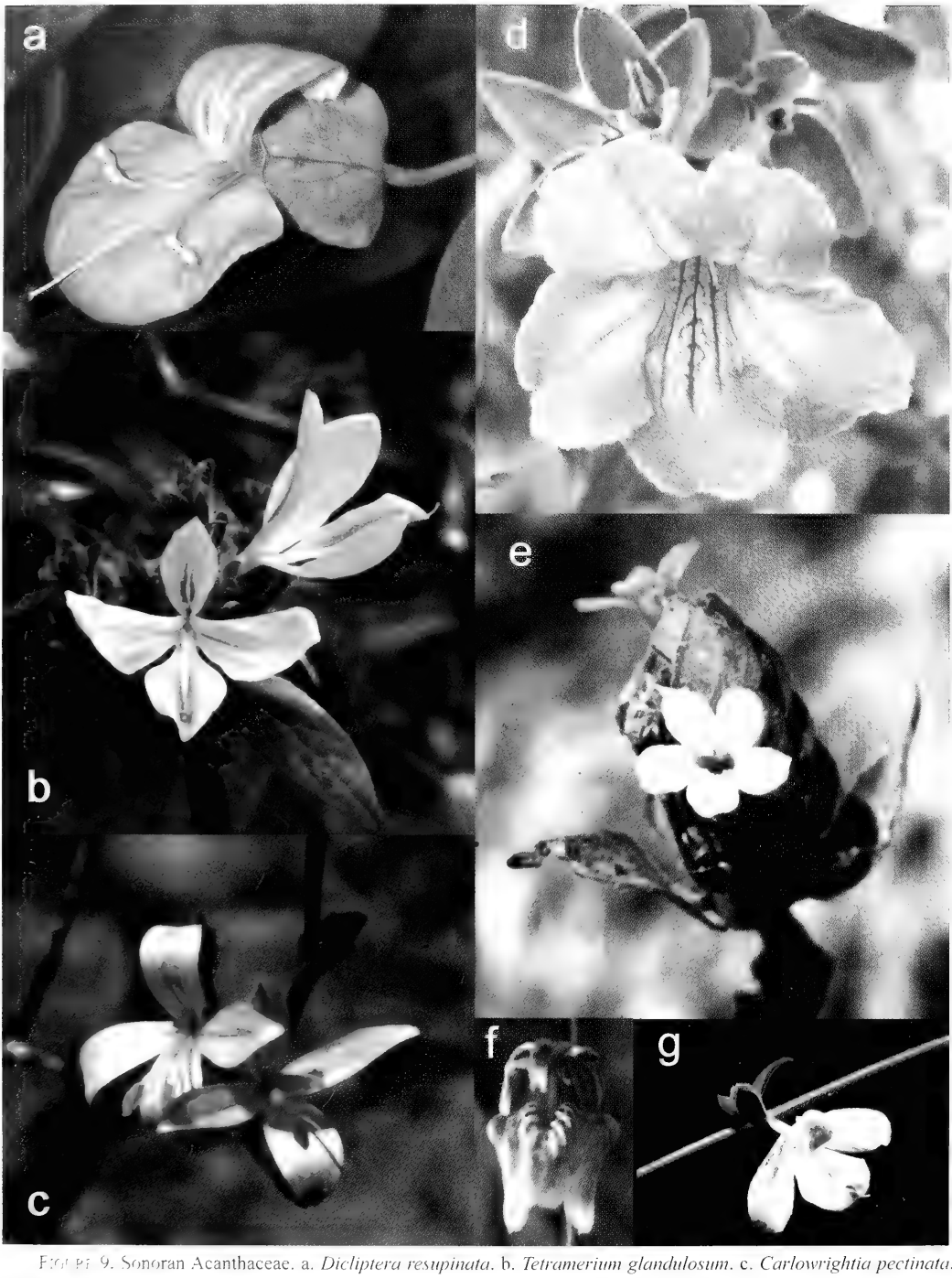


FIGURE 9. Sonoran Acanthaceae. a. *Dicliptera resupinata*. b. *Tetramerium glandulosum*. c. *Carlowrightia pectinata*. d. *Ruellia californica*. e. *Blechum pyramidatum*. f. *Justicia salviiflora*. g. *Henrya insularis*.

Erect to ascending or decumbent perennial herbs or shrubs with cystoliths. Leaves opposite (rarely subopposite). Inflorescence of dichasia in leaf axils, or, more commonly, of dichasiate spikes, racemes, thyrses, or thyrses, the inflorescences sometimes branching and becoming panicles; dichasia alternate or opposite, 1–3 (or more)-flowered, sessile or pedunculate, subtended by a leaf or bract. Flowers homostylous, sessile or pedicellate, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic. Corolla white to cream to yellowish to rose-purple to blue, usually with yellow and maroon or purple markings on upper lip, tube cylindric to subcylindric, throat indistinct, limb pseudopapilionaceous, 2-labiate, or subactinomorphic, upper lip comprising 2 fused lobes, lower lip consisting of 2 similar lateral lobes and a lower-central lobe that is either similar in form to lateral lobes or ± recurved or conduplicate-keeled and enclosing stamens and distal portion of style during anthesis, corolla lobes imbricate in bud. Stamens 2, exserted from mouth of corolla, anthers 2-thecous, thecae equal in size, parallel or subsagittate, subequally inserted on filament, lacking basal appendages, dehiscing toward upper lip of corolla (i.e., flowers stenotribal); pollen (Fig. 3) prolate spheroidal to perprolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed. Capsule stipitate, head flattened to nearly spheric, circular to ovate-elliptic in outline, retinacula present, septae with attached retinacula remaining attached to inner wall of mature capsule. Seeds 2–4, homomorphic or heteromorphic, flat to concavoconvex, smooth or variously ornamented, lacking trichomes. ($x = 18$).

Twenty-six species are recognized in this New World genus. They occur from the southwestern United States throughout Mexico to northwestern Costa Rica and disjunctly to Ecuador and Argentina. With 24 species, Mexico is the center of diversity for *Carlowrightia*.

1. Corolla 5.5–7 mm long, white with maroon veins on all lobes; dichasia borne in leaf axils throughout plant; bracteoles foliaceous, usually petiolate, narrowly ovate to elliptic-lanceolate, 2–12 mm long, 0.7–5 mm wide; seed margin entire; Chihuahuan desertscrub. . . . . *C. texana*
1. Corolla 8–18 mm long, white to yellow with maroon veins (if present) restricted to upper lip; dichasia borne in axils of usually reduced, distal leaves or minute bracts; bracteoles subulate to lanceolate, 1.5–4 (–7) mm long, 0.3–0.8 mm wide; seed margin (entire to) denticulate to dentate to coarsely pectinate; Sonoran desertscrub, thornscrub, and tropical deciduous forest.
   2. Leaf blades petiolate, ovate to elliptic, 1.6–2.5 times longer than wide, margin flat; lower-central lobe of corolla conduplicate-keeled, enclosing stamens and style; thecae maroon turning black; capsule glabrous, head 5.5–7.5 mm long; seeds 4, homomorphic . . . . . *C. arizonica*
   2. Leaf blades sessile to subsessile, linear to narrowly elliptic-lanceolate, 6–29 times longer than wide, margin revolute; lower-central lobe of corolla neither conduplicate nor keel-like, not enclosing stamens and style; thecae golden yellow; capsule pubescent (sometimes only sparsely so at apex), head 3.5–5.5 mm long; seeds 2–4, the third and fourth seeds (when present) usually markedly different in form from others (i.e., partially conduplicate and with a conspicuous pectinate margin). . . . . *C. pectinata*

Carlowrightia arizonica A. Gray, Proc. Amer. Acad. Arts 13:364. 1878. TYPE: UNITED STATES. Arizona: Pinal Co., near Camp Grant, 1867, *E. Palmer 165* (holotype: GH!).

Carlowrightia cordifolia A. Gray, Proc. Amer. Acad. Arts 21:406. 1886. TYPE: MEXICO. Chihuahua: mountains above Batopilas, 1885, *E. Palmer 224* (holotype: GH!; isotypes: K!, NY!, US!).

Carlowrightia glabrata Fernald, Bot. Gaz. (Crawfordsville) 20:536. 1895. TYPE: MEXICO.

Sinaloa: Villa Union, Jan 1893, *F. Lamb 420* (lectotype, designated by Daniel, 1983a: GH!; isolectotypes: DS!, F!, G!, MO!, MSC!, NY!, US!).

Carlowrightia californica Brandegee, Zoe 5:172. 1903. TYPE: MEXICO. Baja California Sur: Comondú, 22 Mar 1889, *T. Brandegee s.n.* (holotype: UC!).

Carlowrightia californica var. *pallida* I.M. Johnst., Proc. Calif. Acad. Sci., ser. 4, 12:1169. 1924. TYPE: MEXICO. Sonora: San Esteban Island, 20 Apr 1921, *I. Johnston 3195* (holotype: CAS!; isotypes: GH!, US!).

See Daniel (1995a) for a complete listing of synonyms.

Phenology. Flowering: February–April, August–October, with a major peak in March-April and a lesser peak in September-October (Fig. 1); fruiting: February–May, September–November.

Distribution and habitats. Southwestern United States (Arizona, California, Texas), Mexico (Baja California, Baja California Sur, Chiapas, Chihuahua, Coahuila, Colima, Guerrero, Jalisco, México, Michoacán, Nayarit, Oaxaca, Puebla, San Luis Potosí, Sinaloa, Sonora), Guatemala, Honduras, Nicaragua, Costa Rica; Sonoran plants occur on slopes, along watercourses, on plains, and in disturbed areas in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Lower Colorado River Valley, Plains of Sonora), thornscrub, and tropical deciduous forests at elevations from sea level to 800 m.

Illustrations. *Trees, Shrubs and Woody Vines of the Southwest*, 934. 1960; *Fieldiana, Botany* 24 (10):350. 1974; *Desert Plants* 5:172. 1984; *Trees and Shrubs of Trans-Pecos Texas*, 399. 1988; *The Jepson Manual, Higher Plants of California*, 127. 1993; *Flora of Chiapas* 4:21. 1995; *Flora of the Gran Desierto and Río Colorado of Northwestern Mexico*, 65. 2000.

Local names. "Anima aguo" (Mayo, *Van Devender et al. 93-1447*); "ánima ogua" (Mayo, *Van Devender et al. 98-2116*); "lemilla" (fide Felger 2000); "palo blanco" (*Van Devender et al. 93-1447*); "rama toro" (fide Gentry 1942, as *C. californica*).

Use. According to Yetman and Van Devender (2002) the Mayo brew leaves into a tea that is taken for fevers. This tea is considered to be more effective when combined with leaves and inflorescences of *Elytraria imbricata*.

Carlowrightia arizonica is widely distributed in Sonora except for the northeastern portion of the state (Fig. 10). Although it occurs in all four subdivisions of the Sonoran Desert in the state, it appears to be rare in the Lower Colorado River Valley. It was noted to occur on Isla Tiburón by Moran (1983), but I have no record of having seen a collection of it from there. It undoubtedly occurs on that island and has been collected on the adjacent Isla San Esteban. Daniel (1983a) provided a description of this widespread and morphologically variable species, including all of its known forms. Forms occurring in the peninsula of Baja California and Chiapas were subsequently described and discussed in more detail by Daniel (1995a, 1997). Four more or less distinctive forms have been noted to occur in Sonora (Daniel 1983a). Many Sonoran plants do not readily correspond to any of them and

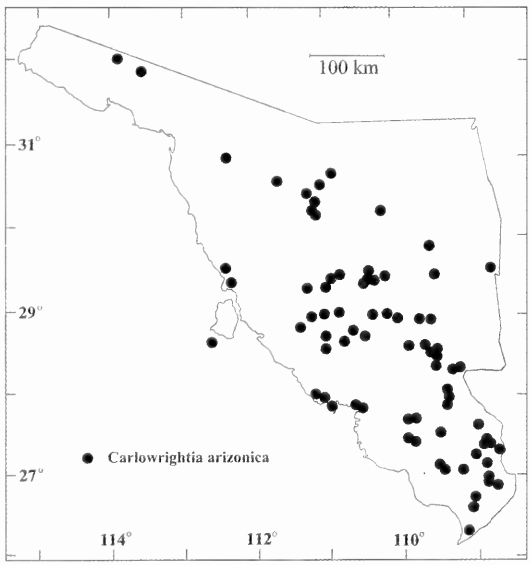


FIGURE 10. Sonoran distribution of *Carlowrightia arizonica*.

others combine characteristics of them in various ways. Perhaps it is more useful to note the range of morphological variation among Sonoran plants of *Carlowrightia arizonica* than to try to assign specimens to one form or another. Among Sonoran plants, habit varies from spreading perennial herbs to erect shrubs; cauline trichomes vary from evenly to bifariously disposed, retrorsely appressed to retrorse to flexuose to erect, eglandular to glandular (inconspicuous in an understory layer), and 0.05 to 1 mm in length; leaf blades vary from lanceolate to ovate to cordate to elliptic, 3 to 85 mm in length, and 1 to 65 mm in width; the inflorescence varies from having dichasia in distal leaf axils to having them in bracteate spicate axes, the axes vary from slender (with dichasia 1 per node) to stout (with dichasia opposite at nodes), bracts vary from 1 to 7 mm in length, and trichomes in the inflorescences vary from eglandular to glandular; calyces vary from 1.5 to 5 mm in length; corollas vary from 9 to 19 mm in length; and capsules vary from 7.5 to 14 mm in length. In any of its guises, this species is readily distinguishable from the other two species of *Carlowrightia* known from Sonora.

Sonoran collections: 9 mi S of Magdalena, *L. Abrams 13242* (DS, F); Sierra Lopez Rancho [37 mi NW of Hermosillo], *L. Abrams 13321* (DS); 2 mi N of Noria, *L. Abrams 13376a* (DS, F); ca. 6 mi E of Alamos, *F. Almeda 2522* (LA); Cerro El Bachoco, NW of Bahía de Guásimas, 27°54', 110°40′W, *T. Burgess et al. 6941* (ARIZ); 2.5 km S de Hermosillo, 29°01′N, 110°57′W, *A. Búrquez & A. Quijada 90-211* (MEXU); along road between Arizpe and Ures, 17.1 mi NE of Ures, ca. 29°30′N, 110°08′W, *T. Daniel 931* (CAS, ENCB, F, GH, MEXU, MICH, MO, NY, TEX, US); along road between Ures and Hermosillo, 17.1 mi SW of Ures, *T. Daniel 939* (CHAPA, DUKE, MICH, UC); along road between Hermosillo and Kino Bay, 2.5 mi E jct. Son. 16 (Calle 4 Sur) to Guaymas, *T. Daniel 941* (CAS, ENCB, F, GH, MEXU, MICH, US); along road between Hermosillo and Sahuaripa, 24.1 mi W of Mazatan, *T. Daniel 945* (ASU, CAS, DUKE, ENCB, F, GH, K, MEXU, MICH, NY, TEX, UC, US); along road between Hermosillo and Sahuaripa, 3 mi W of Mazatan, *T. Daniel 954* (MICH); along road between Mazatan and Sahuaripa, 10.4 mi E of Mazatan, *T. Daniel 962* (ENCB, MEXU, MICH, NY, US); along road between Mazatan and Sahuaripa, 5.9 mi E of Rebeiquito and 3.9 mi W of El Novillo, *T. Daniel 965* (CHAPA, MICH); along road between El Novillo and Sahuaripa, 14.4-17.2 mi E of El Novillo, *T. Daniel 967* (MEXU, MICH), *T. Daniel 971* (ENCB, F, MICH, US); along Son. 16 between Hermosillo and La Colorada, 0.9 mi W of La Colorada, *T. Daniel 974* (MICH); along road between La Colorada and Tecoripa, 12.6 mi E of La Colorada, *T. Daniel 976-980* (MICH); along road between Tecoripa and Tónichi, 9.3 mi E of Tecoripa, *T. Daniel 983* (ENCB, F, GH, MICH, MO, TEX, UC), *984* (CAS, MEXU, MICH, US), *986* (MICH); along road between Tónichi turnoff and Onavas, 4.4 mi S of Tónichi turnoff, *T. Daniel 987* (MICH), *988* (ENCB, MICH), *989* (ENCB, MICH); along road between Tónichi and Onavas, 7.4 mi N of Onavas, *T. Daniel 990* (MICH); along road between Tónichi and Movas, 2.6 mi S of Río Chico, *T. Daniel 992* (ENCB, MICH); along hwy. between Esperanza and Rosario de Tezopaco, 3-30 mi E of jct. with road to Presa Obregón, *T. Daniel 996* (CAS, MEXU, MICH, US), *998* (ENCB, MICH, NY); along road between Navojoa and Alamos, 24.6 mi E jct. Hwy. 15 in Navojoa, *T. Daniel 999* (ENCB, F, GH, MICH, MO, NY, UC); along road between Alamos and San Bernardo, 8.1–33.4 mi NE of Alamos, *T. Daniel 1005* (MEXU, MICH, US), *1006* (MICH); along road from San Bernardo to Chihuahua, 1.8 mi from San Bernardo, *T. Daniel 1007* (MICH), *1008* (MICH); "Microondas Mountain" overlooking Guaymas, along road which is 1.8 mi from Mex. Hwy. 15 on paved road to airport, N of Guaymas, *T. Daniel 1949* (ASU); Mpio. Soyopa, crossing of Río Yaqui with Hwy. 16, 8.5 km W of jct. to Onavas, ca. 28°34′N, 109°33′W, *T. Daniel et al. 8509* (CAS, MEXU); SW of Villa de Seris [= Hermosillo on S side of Río Sonora fide Felger], *F. Drouet et al. 3473* (F); Miramar, NW of Guaymas, *R. Felger 5512* (ARIZ); 5.8 mi S of Imuris on Mex. 15, *R. Felger 7295* (MEXU); Sierra del Viejo, 50 km W of Los Vidrios on Mex. Hwy. 2, ca. 32°09′N, 113°56′W, *R. Felger & M. Dimmitt 85-723* (ARIZ, MEXU); ca. 5 km SW of Ortíz (SE of Guaymas), *R. Felger & N. Gonzales 85-393* (ARIZ, CAS); Pinacate Region, Tinaja de los Papagos, *R. Felger & G. Joseph 86-485A* (ARIZ, MEXU); Cañón Nacapules, ca. 4.5 mi N of Bahía San Carlos, *R. Felger & D. Valdez Z. 84-614* (ARIZ); 2.7 mi E of Tajitos on Mex. Hwy. 2 (between Caborca and Sonoyta), *R. Felger & J. Wright 7420* (ARIZ); El Novillo (E-central Sonora), *R. Felger et al. 84-281* (ARIZ, MEXU); Cañón Las Barajitas, Sierra El Aguaje, ca. 18 km NW of San Carlos, ca. 28°03′N, 111°11′W, *R. Felger et al. 95-194* (ARIZ, CAS); Isla San Esteban, vicinity of Limansur, SE side of island, 29°39′N, 112°34′W, *R. Felger et al. 17650* (CAS); vic. of Rancho Arivaipa,

ca. 8 mi ENE of Pozo Coyote, ca. 29°37′N, 112°17′W, *R. Felger et al. 17833* (ARIZ); Sierra Seri, 29°17′N, 112°08′W, *R. Felger et al. 18131* (ARIZ); 0.2 mi S of San Bernardo, 27°23′N, 108°51′W, *M. Fishbein et al. 932* (ARIZ); 5.9 mi SE of San Bernardo toward mine at San Rafael, 27°21′N, 108°49′W, *M. Fishbein et al. 938* (ARIZ); Mpio. Hermosillo, La Pintada, 50 km S de Hermosillo, 28°35′N, 110°58′W, *A. Flores M. & J. Sánchez E. 5453* (IEB); 15 mi N of Magdalena, *R. Fosberg 7901* (LA, PH); 43 km N of Hermosillo toward Nogales, *T. Frye & E. Frye 2302* (DS, GH, MO, NY, UC, US); Cd. Obregón, *H. Gentry 275* (MICH); Distr. Alamos, Qüirocoba, *H. Gentry 808* (DS, F, MICH); Canyon Sapopa, *H. Gentry 1049* (ARIZ, F); KM 180 S of Nogales, *H. Gentry 16569* (ARIZ, LL, US); Ures, *D. Gold 762* (MEXU); 21 mi E of Tesopaco by old road to Nuri, *D. Goldberg s.n.* (UC); ca. 30 mi S of Hermosillo, *B. Hansen et al. 1379* (LL, MEXU, MICH); Río El Naranjo, N of Taymuco, 27°15′N, 108°43′W, *P. Jenkins & P. Martin 88-253* (ARIZ); Guaymas, *I. Johnston 3100* (CAS, US); Onavas road, 28°28-35′N, 109°31-32′W, *E. Joyal 1363* (CAS, MEXU); Rancho El Aguilar Noria, N of Ures and Santiago, 29°33′N, 110°25-26′W, *E. Joyal 1990* (CAS, MEXU, TEX); 1 mi NW of Navojoa on Hwy. 15, *W. Mahler & J. Thieret 6012* (SMU); Mocúzari, La Cruz, 27°13′N, 109°05′W, *P. Martin s.n.* (ARIZ, CAS); 5 km N of Rosario de Tesopaco, *P. Martin s.n.* (ARIZ); 8 km E of Alamos toward Sabinito Sur, *P. Martin s.n.* (ARIZ); Mazocahui Canyon of the Río Sonora, 66 mi ENE of Hermosillo near Ures, ca. 110°15′N, 29°28′W, *P. Martin & S. Nilsson 38* (S); Estacion Margarita, 10 km NW of Navojoa, 109°29′N, 27°05′W, *P. Martin et al. s.n.* (ARIZ); 18 mi N of Tesopaco, *S. McLaughlin 496* (ARIZ); Mpio. Nacori Chico, El Río Bonito about La Nopalera, *C. Muller 3682* (GH, LL, MICH, UC, US); Agiabampo, *E. Palmer 769* (US); Las Guásimas, *B. Perrill 5355* (ARIZ); 21.6 mi S of Santa Ana, *B. Perrill 5576* (ARIZ); 8 mi E of Moctezuma, 29°50′N, 109°23′W, *F. Reichenbacher 193* (ARIZ); Mpio. Yécora, Arroyo El Encino, ca. 1 km N of Curea, ca. 28°19′N, 109°17′W, *A. Reina G. & T. Van Devender 99-450* (CAS); Mpio. Baviácora, ca. 5 km WSW of Mazocahui on Son. 89, 29°32′N, 110°08′W, *A. Reina G. & T. Van Devender 2000-716* (CAS); Mpio. Arizpe, ca. 19.4 km N of Sinoquipe on Son. 89, 30°19′N, 110°12′W, *A. Reina G. & T. Van Devender 2000-727* (ARIZ, CAS); Mpio. Onavas, Rancho El Palmar, 5 km SE of Río Yaqui on Mex. 16, 28°30′N, 109°24′W, *A. Reina G. et al. 97-93* (ARIZ, CAS, MEXU); Guaymas, *H. Ripley 14270* (CAS, NY); vic. of Hermosillo, *J. Rose et al. 12352* (NY, US); San Carlos Bay, W of Guaymas, near Cerro Los Algodones, ca. 27°58′N, 111°04′W, *A. Sanders et al. 2511* (TEX); near Santa Ana, *F. Shreve 5957* (F); Río San Miguel at first crossing S of Horcasitas, *F. Shreve 6695* (ARIZ, MICH, UC); Río Sonora, 23 mi NE of El Sacatón, *F. Shreve 6701* (ARIZ); ca. 2.2 mi NE of Hwy. 15 (toward microwave tower), ca. 6.9 mi SE of Cd. Obregón, *W. Stevens & M. Fairhurst 2083* (ENCB); ca. 20 mi SE of Altar on Hwy. 2, *R. Straw 2106* (DUKE, SD); Mpio. Yécora, La Concepción, 29°19′N, 109°02′W, *W. Trauba s.n.* (CAS); 4 mi S of Mazocahui, *R. Turner 59-68* (ARIZ); Isla San Esteban, Arroyo Limantur, 28.7°N, 112.6°W, *R. Turner 83-28* (ARIZ); 11 mi E of Hermosillo toward Mazatan, *R. Turner & J. Hastings 65-139* (ARIZ, DS, SD); 4 mi S of Torres, *R. Turner & J. Hastings 65-179* (ARIZ, DS, SD); 8 mi WSW of Santa Ana, *R. Turner & J. Hastings 69-87* (ARIZ); Isla San Esteban, Arroyo Limantur, *T. Van Devender 92-483* (ARIZ, CAS); Mpio. Yécora, El Llano de Curea, 28°18′N, 109°52′W, *T. Van Devender & A. Reina G. 2004-162* (CAS); 21.6 mi S of Santa Ana via Mex. Hwy. 15, *T. Van Devender et al. 84-131* (ARIZ); Río Cuchujaqui, ca. 8 mi SE of Alamos, *T. Van Devender et al. 84-143* (ARIZ); below Guajaráy on Arroyo Guajaráy, 6.5 km WNW of jct. with Río Mayo, 27°36′N, 108°56′W, *T. Van Devender et al. 93-455* (ARIZ, CAS); Mpio. Alamos, Cerro El Chorro, 4 km NW of Yocogigua, 26°49′N, 109°03′W, *T. Van Devender et al. 93-1447* (ARIZ); La Gacela, 26°52′N, 108°52′W, *T. Van Devender et al. 95-57* (TEX); Mpio. San Javier, 2.7 mi E of La Barranca on Mex. Hwy. 16, 28°34′N, 109°40′W, *T. Van Devender et al. 96-6* (ARIZ); Mpio. Soyopa, Río Yaqui bridge on Mex. 16, just S of Tónichi, ca. 28°34′N, 109°33′W, *T. Van Devender et al. 97-1475* (CAS); Ejido Francisco Solis, 7 km (air) ENE of Estacion Luis, ca. 26°35′N, 109°06′W, *T. Van Devender et al. 98-2116* (NY); 8 mi S of Nuri, ca. 27°58′N, 109°18′W, *G. Webster & R. Murphey 24377* (MEXU); S of Magdalena, *Whitehead 48* (ARIZ); 17 mi NE of Cajeme on road to Tezopaco, *I. Wiggins 6397A* (DS, MICH, US); 19 mi NW of Quiriego toward Cajeme, *I. Wiggins 6451* (DS, MICH, US); above second crossing of Río San Miguel just above Fábrica de Los Angeles, *I. Wiggins 7294* (ARIZ, DS, MO, TEX, US); 21 mi S of Divisadero, *I. Wiggins 7480* (DS, US); 27 mi W of Hermosillo toward Kino Bay, *I. Wiggins & R. Rollins 142* (A, ARIZ, DS, MICH, MO, NY, UC, US).

Carlowrightia pectinata Brandegee, Proc. Calif. Acad. Sci., ser. 2, 3:160. 1891. TYPE: MEXICO. Baja California Sur: San José del Cabo, 24 Sep 1890, *T. Brandegee 452* (holotype: UC!; isotypes: F!, GH!, US!).

Carlowrightia fimbriata Brandegee, Proc. Calif. Acad. Sci., ser. 2, 3:161. 1891. TYPE: MEXICO. Baja California Sur: San Pedro, 29 Oct 1890, *T. Brandegee 453* (holotype: UC!; isotypes: CAS!, F!, G!, GH!, MIN!, PH!, US!).

Carlowrightia lanceolata Leonard, Kew Bull. 1938:66. 1938. TYPE: MEXICO. México: Distr. Temascaltepec, Tejupilco, 1340 m, 21 Nov 1932, *G. Hinton 2672* (holotype: K!; isotypes: ENCB!, F!, G!, GH!, K!, MO!, NY!, PH!, RSA!, TEX!, US!).

Phenology. Flowering: September–March; fruiting: October–March.

Distribution and habitats. Western and southern Mexico (Baja California Sur, Colima, México, Morelos, Oaxaca, Sinaloa, Sonora); Sonoran plants occur in canyon bottoms, along watercourses, and on slopes in riparian Sonoran desertscrub (Central Gulf Coast), thornscrub, and tropical deciduous forests at elevations from 30 to 850 m.

Illustrations. Figure 9; *Proceedings of the California Academy of Sciences* 49:326. 1997.

Local name. "Lemilla" (Mexican, *Gentry 1349*).

Daniel (1983a, 1997) provided descriptions of *Carlowrightia pectinata*. The species attains the northern extent of its distribution in central Sonora (Fig. 11). Among Sonoran plants, color of the corolla varies from white (e.g., *Daniel 936*) to yellow (e.g., *Daniel 3381*).

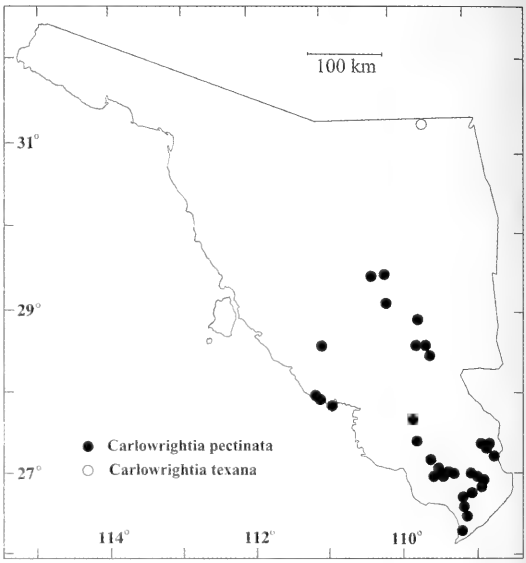


FIGURE 11. Sonoran distributions of *Carlowrightia pectinata* and *C. texana*.

SONORAN COLLECTIONS: 6 km E of Navojoa, *A. Carter & L. Kellogg 3644* (GH, MEXU, UC); 17.1 mi NE of Ures between Arizpe and Ures, *T. Daniel 936* (ASU, CAS, ENCB, GH, MEXU, MICH, NY, US); along Hwy. 16 between Tecoripa and Tónichi, 0.3 mi E of Río Yaqui, *T. Daniel 3345* (CAS, MEXU, NY, US); Arroyo Cuchujaqui, 7.4 mi SE of Alamos on road to Güirocoba, *T. Daniel 3381* (ASU, CAS, MEXU); Mpio. Soyopa, crossing of Río Yaqui with Hwy. 16, 8.5 km W of jct. to Onavas, ca. 28°34′N, 109°33′W, *T. Daniel et al. 8500* (BR, CAS, K, MEXU, MO); Cañón del Nacapule, ca. 6 km N of Bahía San Carlos, ca. 28°10′N, 111°03′W, *R. Felger & A. Búrquez 92-1055* (ARIZ, CAS, TEX); Mpio. Guaymas, Cañón del Nacapule, 6 km N of San Carlos Road, 28°01′N, 111°02′W, *R. Felger & F. Reichenbacher 85-1212* (ARIZ, CAS, MEXU); El Novillo, E-central Sonora, *R. Felger et al. 84-280* (ARIZ, MEXU, TEX); Cañón Nacapules, ca. 4.5 mi N of Bahía San Carlos, *R. Felger et al. 84-603* (ARIZ); Río Mayo Region, Arroyo Infiernillo, near confluence with Arroyo Tepopa, 27°20′N, 108°44′W, *M. Fishbein et al. 993* (ARIZ, CAS); Mpio. Guaymas, Sierra el Aguaje, Aguaje Robinson, ca. 10 km NW de San Carlos, 28°03′N, 111°07′W, *A. Flores M. & O. Gutierrez R. 5086* (ARIZ); vicinity of Fco. Sarabia, Cerro Tasirogojo, 5.5 km SE of Melchor Ocampo, 26°31′N, 109°08′W, *S. Friedman & E. Espinosa 227-94* (ARIZ); Mesa Masiaca, 6.5 km WNW San José de Masiaca, 26°46′N, 109°18′W, *S. Friedman & J. Freeh 376-94* (ARIZ, TEX); vicinity of Sirebampo, 9.5 km S on Mex. Hwy. 15 from Las Bocas road turnoff, 3.5 km W on Sirebampo road, 11.5 km S of San José de Masiaca, 26°39′N, 109°15′W, *S. Friedman & J. Zittere 88-95* (ARIZ); Distr. Alamos, Pichiquate Canyon, *H. Gentry 966* (DS), *966.M* (MICH); San Bernardo, Río Mayo, *H. Gentry 1349* (ARIZ, F, MEXU); Curohui, Río Mayo, *H. Gentry 2144* (ARIZ, F, GH, MEXU, MO, S, UC, US, WIS); Cerro de Bayájori, 12 mi W of Navojoa, *H. Gentry 7946*

(ARIZ); Sierra Bojihuacame, SE of Cd. Obregón, *H. Gentry 14533* (ARIZ, LL); Tepustete microwave tower, W of Alamos, *P. Jenkins s.n.* (ARIZ, CAS); San Carlos Bay, *I. Johnston 4388* (CAS); Onavas road, 28°28-35′N, 109°31-32′W, *E. Joyal 1385* (CAS, MEXU, TEX); Mazocahui Canyon of the Río Sonora, 66 mi ENE of Hermosillo near Ures, ca. 110°15′N, 29°28′W, *P. Martin & S. Nilsson 37* (S); Microondas Masiaca, 7 km W of Masiaca, 26°46′, 109°18′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); Estación Margarita, 10 km NW of Navojoa, 27°08′N, 109°29′W, *P. Martin et al. s.n.* (ARIZ, CAS); turn to La Viñateria on road between Taymuco and Las Chinacas, *P. Martin et al. s.n.* (ARIZ); along Hwy. 15 ca. 23 mi N of Navojoa, *D. Norris et al. 20083* (CAS, MEXU, MO); W of Guaymas, *E. Palmer 259* (ARIZ, C, MICH, S, US); Agiabampo, *E. Palmer 764* (ARIZ, MICH, S, UC, US); Onavas, ca. 28°28′N, 109°32′W, *A. Rea 1221* (ARIZ); Mpio. Soyopa, NE side of Río Yaqui bridge on Mex. 16, just S of Tónichi, ca. 28°34′N, 109°33′W, *A. Reina G. et al. 97-42* (CAS); Cerro Prieto, 8.6 mi E of Navojoa on road to Alamos, ca. 27°15′N, 109°17′W, *A. Sanders et al. 4617* (ARIZ, TEX); Mpio. Alamos, Cerro La Luna, ca. 14 km NW of Alamos, ca. 27°07′N, 109°02′W, *A. Sanders et al. 13262* (CAS, TEX); 40 mi NE of Cajeme, *F. Shreve 6156* (ARIZ, F); Cerro Prieto, 1.3 mi up road to microwave tower from road between Navojoa and Alamos, *E. Smith 3966* (CAS, MEXU, TEX); Nacopuli Canyon, 28°01′N, 110°03′W, *G. Starr & C. Starr 216* (ARIZ); Arroyo Gochico, ca. 14 km E of San Bernardo, 27°24′N, 108°41′W, *V. Steinmann et al. 601* (ARIZ, CAS, MEXU, MO); Mpio. Navojoa, Cerro Prieto, ca. 14 km E of Navojoa, ca. 27°05′N, 109°17′W, *V. Steinmann 1299* (ARIZ, CAS, IEB, MO, TEX); Cañón La Pintada, ca. 78 km N of Guaymas on Mex. Hwy. 15, Cerro Bola, Sierra Libre, *R. Van Devender & T. Van Devender 84-23* (ARIZ); Río Cuchujaqui, ca. 8 mi SE of Alamos, *T. Van Devender & R. Nishida s.n.* (ARIZ); Güirocoba crossing of Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56′N, 108°53′W, *T. Van Devender & R. Van Devender 93-156* (ARIZ, CAS); below microwave tower on Cerro Prieto, ca. 9 mi E of Navojoa, 27°05′N, 109°17′W, *T. Van Devender et al. 93-243* (ARIZ, CAS); Cerro las Tatemas, below Microondas La Luna, 13.8 km NW of Alamos, 27°07′N, 109°02′W, *T. Van Devender et al. 93-341* (ARIZ, CAS, TEX); Mpio. Alamos, Cerro El Chorro, 4 km NW of Yocogigua, 26°49′N, 109°03′W, *T. Van Devender et al. 93-1499* (ARIZ, CAS); La Gacela, 26°52′N, 108°52′W, *T. Van Devender et al. 95-57* (ARIZ); Mpio. Soyopa, NE side of Río Yaqui bridge on Mex. 16 just S of Tónichi, ca. 28°34′N, 109°33′W, *T. Van Devender et al. 97-1476* (ARIZ, CAS, MEXU, TEX); Mpio. Ures, SSW of Satebuche, ca. 10 km NW of Nacori Grande, E. slope of Sierra de Mazatan, 29°07′N, 110°08′W, *T. Van Devender et al. 2004-483* (CAS); San Javier, cañón entre los cerros El Potrerito y Los Amoles, 7 km S del poblado, 28°32′N, 109°45′W, *L. Varela E. 96-312* (MEXU); 35 mi NE of Cajeme on road to Tesopaco, *I. Wiggins 6415B* (DS, MICH, US).

Carlowrightia texana Henr. & T.F. Daniel, Madroño 26:27. 1979. TYPE: U.S.A. Texas: Val Verde Co., along Hwy. 163, 6 mi N of Juno, 19 Jun 1957, *D. Correll & M. Johnston 18254* (holotype: LL!; isotypes: GH!, NY!, SMU!).

Phenology. Flowering: September; fruiting: September.

Distribution and habitat. Southern and southwestern United States (New Mexico, Texas), northern Mexico (Chihuahua, Coahuila, Nuevo León, San Luis Potosí, Sonora); Sonoran plants occur on a roadside in Chihuahuan desertscrub at an elevation of 1215 m.

Illustrations. *Madroño* 26:28. 1979; *Trees and Shrubs of Trans-Pecos Texas*, 401. 1988.

Daniel (1983a) provided a description of *Carlowrightia texana*. It was only recently (in 2002) collected in Sonora for the first time. The locality in northeastern Sonora (Fig. 11) represents the western extent of the known distribution of the species. It should be sought in similar habitats in nearby Arizona where its occurrence is likely, but has yet to be documented.

Sonoran collection: Mpio. Agua Prieta, W edge of Agua Prieta on Mex. 2, ca. 31°19′N, 109°34′W, *T. Van Devender et al. 2002-617* (CAS).

Dicliptera Juss.

Dicliptera Juss., Ann. Mus. Natl. Hist. Nat. 9:267. 1807, nom. cons. TYPE: *Dicliptera chinensis* (L.) Juss. (≡ *Justicia chinensis* L.).

Diapedium K.D. Koenig, Ann. Bot. 2:189. 1805 ("1806"), nom. rej. TYPE: *Diapedium chinense* (L.) K.D. Koenig (≡ *Justicia chinensis* L.).

Solenochasma Fenzl in J. Jacquin, Ecl. Pl. Rar. 2:1. 1844. TYPE: *Solenochasma assurgens* (L.) Fenzl (≡ *Justicia assurgens* L.).

Dactylostegium Nees in Martius, Fl. Bras. 9:162. 1847. TYPE: *Dactylostegium sparsiflorum* Nees.

Erect to ascending or decumbent perennial herbs or shrubs with cystoliths, young stems ± distinctly 6-angled in cross-section. Leaves opposite. Inflorescence of axillary cymes (= modified dichasia ?) bearing 1 or more, bracteolate cymules; cymes alternate or opposite, subtended by paired bracts, sessile or pedunculate in leaf axils or in axils of inflorescence bracts forming a terminal spikelike thyrse or panicle of thyrses; cymules sessile or pedunculate, comprising an involucre of several pairs of bracteoles, outermost pair usually conspicuous and larger than inner (often hyaline) pair(s), cymule bracteoles of a pair equal or unequal in size. Flowers 1-several per cymule, homostylous, sessile. Calyx deeply 5-lobed, usually reduced and hyaline, lobes equal to subequal. Corolla often resupinate (i.e., tube twisted 180°; elsewhere sometimes twisted 360°), pink to purple, red, white, or blue, often with pink to purple markings, tube cylindric to gradually expanded distally but lacking a distinct throat, limb 2-labiate, upper lip comprising 2 fused lobes, entire to emarginate at apex, lower lip entire to shallowly 3-lobed (normal position of lips reversed when corolla resupinate), corolla lobes imbricate in bud. Stamens 2, exserted from mouth of corolla or rarely included in corolla tube, anthers 2-thecous, thecae equal to subequal in size, parallel to perpendicular, equally to unequally inserted on filament, lacking basal appendages (in Mexican species; elsewhere rarely with lower theca minutely appendaged at base), dehiscing toward lower lip (i.e., flower nototribal) in species with corollas either not resupinate or twisted 360°, dehiscing toward upper lip (i.e., flower stenotribal) in species with resupinate corollas; pollen (Fig. 12) euprolate to perprolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate; staminodes 0. Style exserted from mouth of corolla or rarely included in corolla tube, stigma 2-lobed, lobes equal. Capsule substipitate to stipitate, head ellipsoid to obovoid, retinacula present, septa with attached retinacula separating elastically and rising from inner wall of mature capsule. Seeds 2-4, homomorphic, subreniform to lenticular. (x = 40 in New World taxa; x = 13 or 15? in Old World taxa).

Although about 300 species have been described from tropical and temperate regions of the world, the number of species usually given is about one-half that number or fewer. The genus is in need of critical taxonomic study. About 20 species occur in Mexico.

Dicliptera resupinata (Vahl) Juss., Ann. Mus. Natl. Hist. Nat. 9:268. 1807. *Justicia sexangularis* Cav., Icon. 3:2. 1795, non L. (1753). *Justicia resupinata* Vahl, Enum. Pl. 1:114. 1804. *Diapedium resupinatum* (Vahl) Kuntze, Revis. Gen. Pl. 2:485. 1891. TYPE: not designated (see discussion in Daniel, 1997).

Dicliptera pseudoverticillaris A. Gray, Proc. Amer. Acad. Arts 20:308. 1885. TYPE: MEXICO. Sonora: valley of the Altar, 2 Apr 1884, *C. Pringle 27* (lectotype, designated by Daniel, 1997: GH!).

Dicliptera torreyi A. Gray, Proc. Amer. Acad. Arts 20:309. 1885. *Diapedium torrey* (A. Gray) A. Heller, Cat. N. Amer. pl. 7. 1898. TYPE: UNITED STATES. Arizona: unspecified collections of Thurber, Wright, Schott, Rothrock, Lemmon, and Pringle were cited (syntypes, see discussion in Daniel 1997).

Dianthera sexangularis Sessé & Moc., Pl. Nov. Hisp. 5. 1887. TYPE: Icones Florae

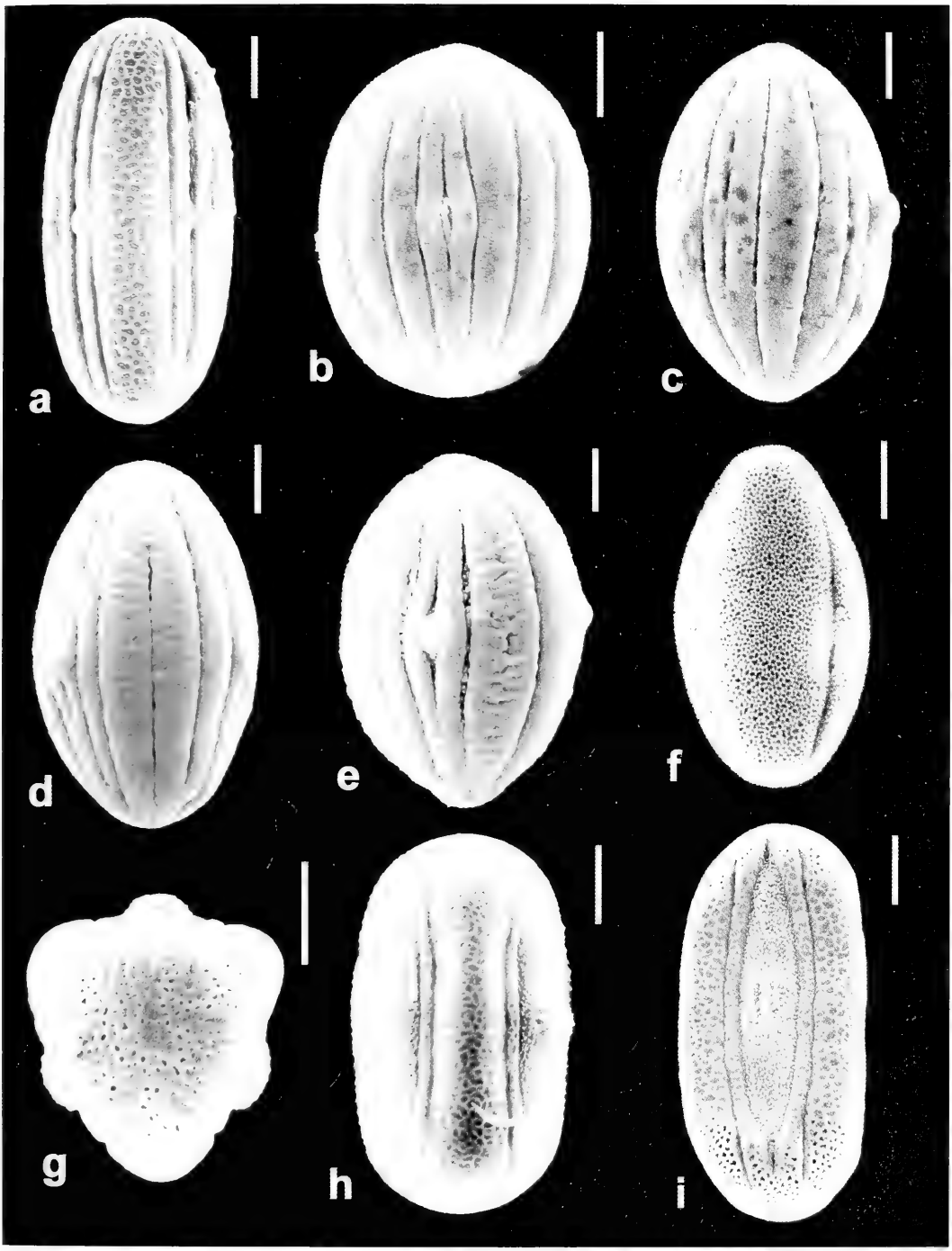


FIGURE 12. Pollen of Sonoran Acanthaceae. a. *Dicliptera resupinata* (*Daniel 1947*), interapertural view. b. *Dyschoriste decumbens* (*Jones 24437*), apertural view. c. *D. xylopoda* (*Wilbur & Wilbur 2137*), interapertural view. d. *D. hirsutissima* (*Daniel et al. 8559*), interapertural view. e. *D. hirsutissima* (*Daniel et al. 8559*), apertural view. f. *Elytraria imbricata* (*Porter 297*), interapertural view. g. *Henrya insularis* (*Daniel 2116*), polar view. h. *H. insularis* (*Daniel & Bartholomew 4822*), interapertural view. i. *H. insularis* (*Daniel & Bartholomew 4731*), apertural view. Scales = 10 μm.

Mexicanae no. 22. Original plate preserved at Hunt Institute for Botanical Documentation, Pittsburgh, Pennsylvania, USA (lectotype, designated by Daniel, 1997).

Dicliptera formosa Brandegee, Proc. Calif. Acad. Sci., ser. 2, 3:162. 1891. TYPE: MEXICO. Baja California Sur: summit of Sierra de San Francisquito, 20 Oct 1890, *T. Brandegee 455* (holotype: UC!; isotypes: GH!, NY).

Dicliptera resupinata var. *orbicularis* B.L. Rob. & Seaton, Proc. Amer. Acad. Arts 28:114. 1893. TYPE: MEXICO. Jalisco: barranca near Guadalajara, Oct 1891, *C. Pringle 5169* (holotype: GH; isotype: MEXU!).

Phenology. Flowering: throughout the year, with peaks in March-April and September-October (Fig. 1); fruiting: September–June.

Distribution and habitats. Southwestern United States (Arizona, New Mexico), western Mexico (Baja California Sur, Chihuahua, Colima, Durango, Guerrero, Jalisco, Michoacán, Nayarit, Sinaloa, Sonora, Zacatecas); Sonoran plants occur on rocky slopes, sand dunes, and along watercourses in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Lower Colorado River Valley, Plains of Sonora), Chihuahuan desertscrub, palm oases, thornscrub, grasslands, tropical deciduous forests, and oak woodlands at elevations from sea level to 1330 m.

Illustrations. Figure 9; *Flora of Baja California*, 190. 1980; *Proceedings of the California Academy of Sciences* 49:331. 1997.

Local names. "Alfalfilla" (fide Van Devender et al. 2000; *Varela & Cuameca 96-496, 97-56*); "himarí" (Wahrio, *Gentry 1075*); "kokpondam" (Pima Bajo, *Rea 1231*); "puenta cita" (Mexican, *Rea 1231*); "rama del toro" (*Van Devender et al. 94-226*); "yerba de la mula" (Mexican, *Rea 1231*).

Daniel (1997) provided a description of this species and discussed some of its morphological variation in northwestern Mexico. In Sonora, length of the corolla varies from 19–34 mm, and length of the outer cymule bracteoles varies from 6–20 mm. Plants with larger bracteoles and corollas occur in vicinity of Guaymas and San Carlos. *Dicliptera resupinata* occurs nearly throughout Sonora (Fig. 13), but is not known from the northwestern portion of the state.

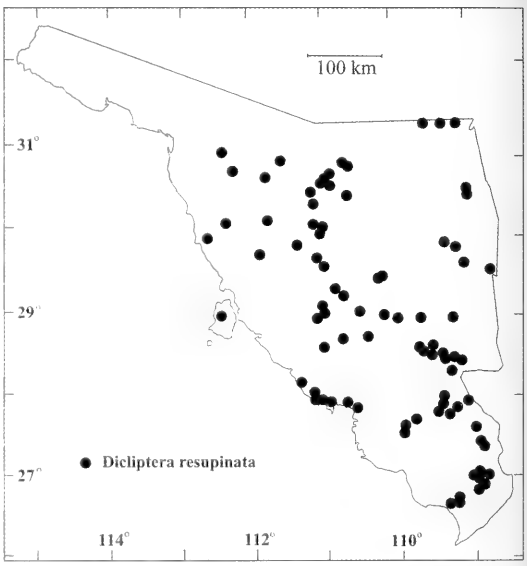


FIGURE 13. Sonoran distribution of *Dicliptera resupinata*.

SONORAN COLLECTIONS: 3 mi S of Magdalena, *L. Abrams 13213* (DS, F); Camou, *L. Abrams 13273* (DS); 1 mi S of Camou on road to Poza, *L. Abrams 13283* (DS); San Miguel River, 15 mi NE of Alamitos near Labor, L. *Abrams 13359* (DS); puerto de Hermosillo, *G. Black 36-6773* (US); Mpio. Guaymas, 12.7 mi S of Puente Douglas across Guaymas Bay, *D. Breedlove 1477* (DS); Mpio. Hermosillo, 7 mi W of Hwy. 15 along southern road to Bahía Kino, *D. Breedlove 15939* (DS, ENCB); N end of Sierra Libre, 28°35′N, 110°58′W, *T. Burgess & R. Turner 6722* (ARIZ, MEXU); Microwave Mountain, N of Guaymas, *M. Burgess et al. s.n.* (ARIZ); San Javier, microondas en el Cerro El Durazno, 28°37′, 109°45′W, *A. Búrquez 94-009* (MEXU); 2.5 km S de Hermosillo, 29°01′N, 110°57′W, A. Búrquez & I. Granillo 93-94 (MEXU), *A. Búrquez & A. Quijada 91-11* (MEXU), *91-129* (MEXU); Cañón Tepoca, KM 177 de la Carr. Fed. 16, 28°27′N, 109°16′W, *A. Búrquez et al. 94-134* (MEXU); Mpio. Benjamín Hill, ca. 22 km N of Benjamín Hill, *C. Cowan*

et al. 5523 (CAS, MEXU, NY, TEX); 3 mi W of Mazatan, between Hermosillo and Sahuaripa, *T. Daniel 946* (CAS, ENCB); between Mazatan and Sahuaripa, 10.4 mi E of Mazatan, *T. Daniel 963* (ASU, CAS, MEXU); "microondas mountain" overlooking Guaymas, along road to top which is 1.8 mi from Hwy. 15 on road to airport N of Guaymas, *T. Daniel 1947* (ASU, CAS, NY, US); Río Cuchujaqui, ca. 8 mi SE of Alamos, *T. Daniel & M. Butterwick 3200* (ASU, CAS); between Esperanza and Rosario de Tezopaco, 3.17 mi SE jct. Hwy. 15, *T. Daniel 3360* (CAS); along road to El Tezal, 0.2 mi N hwy. between Navojoa and Alamos, 2.6 mi W of Alamos, *T. Daniel 3376* (CAS); near San Carlos (NW of Guaymas), ca. 2 mi E of town, *T. Daniel 3972* (CAS); Mpio. Onavas, Rancho La Mula, near Hwy. 16, 18.9 km SE jct. to Onavas, ca. 28°29′N, 109° 22′W, *T. Daniel et al. 8552* (CAS); Mpio. Yécora, along road between San Nicolás and Nurí, just S of Curea, ca. 24 km SW jct. Hwy. 16, ca. 28°19′N, 109°17′W, *T. Daniel et al. 8582* (CAS); Bahía San Carlos, *E. Dawson 1071* (F); S of Villa de Seris, *F. Drouet & D. Richards 3766* (F); mountain W of Alamos, *F. Drouet & D. Richards 4003* (F); S of Villa de Seris, *F. Drouet et al. 3432* (F); 20 mi NE of Ures, *F. Drouet et al. 3591* (DS, F, US); Rancho San Jorge, W of Hermosillo, ca. 29°44′N, 111°51′W, *R. Felger 6915* (ARIZ); 0.8 km E of Las Guásimas, *R. Felger & R. Devine 85-293* (ARIZ, MEXU); N end of Bahía San Carlos, ca. 0.5 mi inland, *R. Felger & C. Lowe 2686* (ARIZ); 9 mi E of Empalme end of Douglas Bridge on Mex. 15, then 2.5 mi S of Hwy. on Playa del Sol road, 27°54′N, 110°41′W, *R. Felger & F. Reichenbacher 85-1110* (ARIZ, CAS, MEXU); Cañón las Barajitas, Sierra El Aguaje, ca. 18 km NW of San Carlos, ca. 28°04′N, 111°12′W, *R. Felger & M. Wilson 95-175* (ARIZ, CAS); El Novillo (E central Sonora), *R. Felger et al. 84-265* (ARIZ); Ensenada Grande, ca. 0.5 km inland from S end of bay [NW of Guaymas], *R. Felger et al. 11407* (ARIZ); Ensenada Grande (= Bahía San Pedro), *R. Felger et al. 11571* (ARIZ, ENCB), *11631* (ARIZ); Isla Tiburón, ca. 13 mi S of Tecomate, ca. 28°57′N, 112°27′W, *R. Felger et al. 12365* (ARIZ, ENCB), *17309* (ARIZ); Isla Tiburón, ca. 13 mi S of Tecomate, ca. 28°57′N, 112°27′W, *R. Felger et al. 17309* (ARIZ); 4 mi W of Alamos toward Navojoa, *J. Fish 7* (UC); 3.2 mi SE of San Bernardo to mine at San Rafael, 27°22′N, 108°49′W, *M. Fishbein et al. 936* (ARIZ); Mpio. Arivechi, 2 km NW de Arivechi, carr. a Sahuaripa, 28°58′N, 109°10′W, *A. Flores M. & M. Arvizo Y. 4756* (ARIZ, MEXU); 75 km N of Hermosillo toward Nogales, *T. Frye & E. Frye 2307* (GH, NY, UC, US); San Lorenzo, *H. Gentry 226* (DS, SMU); Distr. Alamos, Canyon Estrella, *H. Gentry 379* (ARIZ, DS); Distr. Alamos, Saucito Canyon, *H. Gentry 687* (DS, US); Canyon Sapopa, *H. Gentry 1075* (ARIZ, US); Canyon Sapopa, Río Mayo, *H. Gentry 1075* (F, GH, MO, WIS); San Bernardo, Río Mayo, *H. Gentry 1160* (ARIZ, F, UC); Alamos, *H. Gentry et al. 19347* (ARIZ, US); ca. 0.5 km inland from Algodones Bay, Guaymas area, *D. Goldberg s.n.* (ARIZ); Granados, *C. Hartman 237* (GH, NY, PH, UC, US); 4 mi W of Rancho San Nicolás on road between Nuri and Yécora, *P. Hubbell s.n.* (ARIZ); N of Cd. Obregón, *P. Jenkins s.n.* (ARIZ); San Carlos Bay, *I. Johnston 4363* (CAS, GH); N of Alamos between Cerros el Cucurucho and El Aguaje, 27°04-05′N, 108°58′W, *E. Joyal 1342* (CAS, MEXU); Las Cabras, ESE of Alamos, 27°00′N, 108°55′W, *E. Joyal 1522* (CAS); Agua Caliente drainage between Rancho El Alamo and Buena Vista, 29°36′N, 108°56′W, *E. Joyal & M. Silva* C. *1772* (CAS, MEXU); 4 mi W of Caborca toward Tajitos, *D. Keck 4050* (DS, US); 3 mi NW of Tajitos (25 mi NW of Caborca) toward Quitovac, *D. Keck 4087* (DS, GH, UC, US); Alamo, Magdalena, *P. Kennedy 7056* (US); Mpio. Hermosillo, Hwy. 21, 25 km E of Hwy. 15, ca. 3 km E of San Francisco de Batuc, 29°15′N, 110°40′W, *G. Levin 2186* (CAS, MEXU); Badehuachi, *C. Lloyd 441* (GH, US); KM 145 on Hwy. 15 between Santa Ana and Hermosillo, *M. Luckow 2978* (MEXU, TEX); Cernas, *D. MacDougal & F. Shreve 7* (GH, US); 34 mi NE of Cajeme on road to Tesopaco, *T. Mallery s.n.* (ARIZ); La Fundicion camp, road to San Pedro, 27°01′N, 108°45′W, *P. Martin s.n.* (ARIZ); Guaymas, 2 mi below microwave, 27°57′N, 110°54′W, *P. Martin s.n.* (ARIZ); 1 km NE of Bachoco, 26°44′N, 109°21′W, *P. Martin & M. O'Rourke s.n.* (ARIZ, MEXU, MO); Micoondas Masiaca, 26°46′N, 109°18′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); near Mesa La Lagunita on road to Sierra Obscura, 5 mi W of Rancho Agua Blanca, *P. Martin & R. Robichaux s.n.* (ARIZ); Arroyo San Pablo, ca. 2.5 mi S of Guajaráy, 27°35′N, 108°51′W, *P. Martin & P. Sundt s.n.* (ARIZ); Cerro Verde, along Río San Javier, 28°34′N, 109°44′W, *P. Martin et al. s.n.* (CAS); Rancho La Presa (Tetagiosa) and road N 10 km to Alamos-Navojoa road, 27°00'–03′N, 109°04–06′W, *P. Martin et al. s.n.* (ARIZ); 2 mi SE of Agua Fria on road to La Brisca, NE of Cucurpe, *N. McCarten & T. Van Devender 2252* (ARIZ, ENCB); 5 mi N of Tezopaco, *S. McLaughlin 488* (ARIZ); Guadalupe Cañón, *E. Mearns & E. Merton 2037* (DS, US); San Pedro Bay, 30°03′N, 111°17′W, *R. Moran 4039* (DS); Mpio. Nacori Chico, El Río Bonito about La Nopalera (W slope of Sierra Madre), *C. Muller 3632* (F, GH, LL, UC); Magdalena, *C. Orcutt 1349* (US); Yaqui River, *E. Palmer 5* (GH, NY, PH); Alamos, *E. Palmer 632* (GH, NY, US); Yaqui River, *E. Palmer s.n.* in 1869 (US);

6 mi N of Obregón, *K. Parker 8212* (ARIZ, CAS); 2 mi NE of ariport, NW of Hermosillo, *D. Pinkava et al. 942* (ENCB); Torres, *C. Purpus 410* (UC); 6 km WNW of San Carlos, 27°57′N, 111°06′W, *M. Quinn & P. Sundt 071* (ARIZ); Onvas, along Río Yaqui, 28°28′N, 109°32′W, *A. Rea 1231* (ARIZ); Ensenada Chica, 15.1 mi W of Hermosillo-Guaymas Hwy., 6 mi S of San Augustín Beach turnoff, 28°07′N, 111°17′W, *F. Reichenbacher 243* (ARIZ); 14 mi by Tecolote road W of Mex. Hwy. 15, 29°48′N, 111°16′W, *F. Reichenbacher 1022A* (ARIZ); Mpio. Yécora, Restaurant La Palmita, 9.5 km W of Restaurant Puerto de la Cruz on Mex. 16 (KM 258 E of Cd. Obregón), N side of Mesa el Campanero, 28°22′N, 109°04′W, *A. Reina G. & T. Van Devender 2000-796* (CAS); Mpio. Opodepe, Arroyo San Cayetano, E side of Querobabi, 30°03′N, 111°01′W, *A. Reina G. & T. Van Devender 2001-595* (CAS); 2.7 km WNW of Tepoca on Mex. 16, ca. 28°28′N, 109°16′W, *A. Reina G. et al. 98-255* (NY); Playa San Carlos, NW of Guaymas, *H. Ripley 14258* (CAS, NY); Arroyo San Xavier between Rancho Lo de Campo and Rancho Panzicola, *R. Rondeau s.n.* (ARIZ); ca. 5 mi below Minas Nuevas, *J. Rose et al. 12674* (NY, US); Sierra de Alamos, vicinity of Alamos, *J. Rose et al. 13001* (NY, US); Mpio. Alamos, Alamos Wash on E side of Alamos, ca. 27°02′N, 108°55′W, *A. Sanders & G. Helmkamp 13306* (TEX); near Mina Sahuarito, S of Cerro San Luis, 20 mi SW of Trincheras, ca. 30°09′N, 111°43′W, *A. Sanders et al. 3587* (MEXU); near Sta. Magdalena, *Scott s.n.* (F); Sta. Magdalena y Imuris, *Schott s.n.* (F); 14 mi W of Pozo Serna on road to Puerto Libertad, *F. Shreve 5452* (ARIZ); near Santa Ana, *F. Shreve 5956* (ARIZ, F); Magdalena Canyon, 11 mi NE of Imuris, *F. Shreve 6626* (ARIZ, F, GH); 26 mi NW of Caborca, *F. Shreve 7556a* (ARIZ); ca. 3-4 mi NW of San Carlos, *E. Smith 3969* (CAS, MEXU, TEX); 25 mi E of La Motica on road to Tezopaco, *W. Spaulding 75-3-16* (ARIZ); Sierra Madre Occidental, ca. 4 mi N of Santa Ana on road to Yepachic, *W. Spaulding 75-3-52* (ARIZ); 2.6 mi ESE of Alamos, 27°01′N, 108°54′W, *G. Starr & D. Palzkill 322* (ARIZ); 18.5 mi SE of Río Yaqui crossing on Mex. Hwy. 16, *G. Starr & C. Starr 189* (ARIZ); Microondas Hill, Guaymas, *G. Starr & C. Starr 195* (ARIZ); Mpio. Alamos, La Huerta, 1.8 km NNW of Alamos toward San Bernardo, ca. 27°02′N, 108°57′W, *V. Steinmann et al. 9324* (ARIZ, MEXU); Río Yaqui, *R. Studhalter 1379* (US); Xorim, *R. Studhalter 1447* (US); Agua Prieta, *J. Thornber s.n.* (ARIZ); Magdalena, *G. Thurber 1028* (F, GH); San Carlos, *L. Toolin & K. Roever 562* (ARIZ); 1.5 mi N of Bavispe, *R. Turner & J. Hastings 65-45* (ARIZ, DS); 31 mi E of Hermosillo toward Mazatan, *R. Turner & J. Hastings 65-154* (ARIZ, DS); 2.5 mi SW of Atil, 30.8°N, 111.6°W, *R. Turner & J. Hastings 72-31* (ARIZ, MEXU); 59 km ESE of Hermosillo on Son. 16, 28°45′N, 110°28′W, *T. Van Devender & V. Markgraf s.n.* (ARIZ); near Rancho Agua Fria on Río Saracachi, E of Cucurpe, *T. Van Devender & C. Miksicek s.n.* (ARIZ); Playa La Manga, N of San Carlos Bay, *T. Van Devender & F. Nishida s.n.* (ARIZ); ca. 4 mi SE of Magdalena, *T. Van Devender & K. Schmidt s.n.* (ARIZ); Güirocoba crossing of Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56′N, 108°53′W, *T. Van Devender et al. 92-940* (ARIZ); El Ranchería crossing of Río Cuchujaqui, ca. 22.5 km S of Alamos on road to El Chinal, 26°51′N, 108°55′W, *T. Van Devender et al. 93-52* (ARIZ, CAS); Mpio. Navojoa, Arroyo Masiaca, ca. 0.5 km N of Teachive de Masiaca, 26°48′N, 109°14′W, *T. Van Devender et al. 93-956* (ARIZ); El Rincón Viejo, ca. 3.4 km N of Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 93-1063* (ARIZ); Cerro Piedra Boluda, ca. 1 km NE of El Rincón Viejo, ca. 4.5 km N of Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 94-226* (ARIZ); Mpio. Yécora, El Barranco de la Vinateria Los Sauces, 4 km S of Mex. 16 on road to Santa Ana, 28°23′N, 109°08′W, *T. Van Devender et al. 97-228* (MEXU); Mpio. Agua Prieta, Arroyo Gallardo, 8 km E of Agua Prieta on Mex. 2, 31°19′N, 109°23′W, *T. Van Devender et al. 2002-635* (CAS); 3.9 mi SW of Mazocahui, *T. Van Devender et al. s.n.* (ARIZ); San Javier, entre los cerros El Potrerito y Los Amoles, 7 km S del poblado, 28°32′N, 109°45′W, *L. Varela & E. Cuamea 96-496* (MEXU); San Javier, 28°36′N, 109°45′W, *L. Varela & E. Cuamea 97-56* (MEXU); 8 mi S of Nuri, ca. 27°58′N, 109°18′W, *G. Webster & R. Murphey 24376* (MEXU); Bavispe, Río Bavispe, *S. White 2886* (ARIZ, GH, US); Hacienda Oquitoa, 6 mi E of Altar, *I. Wiggins 5975* (DS, UC, US); Tinaja Picu in Picu Mts., 2 mi N of monument on N side of Libertad Road, *I. Wiggins 6052* (DS, US); Rancho San Ignacio, *I. Wiggins 6107* (DS, UC, US); 6 mi S of Carbo, from hwy. to San Miguel, *I. Wiggins 6237* (DS); road to Remedios, 3 mi from jct. Cananea Road, *I. Wiggins 7091A* (DS); ca. 2 mi E of Rancho Noria de Navaso, *I. Wiggins 7284* (DS, US).

Dyschoriste Nees

Dyschoriste Nees in N. Wallich, Pl. Asiat. Rar. 3:75, 81. 1832. LECTOTYPE (Britton & Brown, Ill. Fl. N. U.S., ed. 2, 3:240. 1913): *Dyschoriste depressa* Nees.

Calophanes D. Don in Sweet, Brit. Fl. Gard. ser. 2, 2:t. 181. 1833. TYPE: *Calophanes oblongifolia* (Michx.) D. Don (≡ *Ruellia oblongifolia* Michx.).

Linostylis Fenzl ex Sond., Linnaea 23:94. 1850. TYPE: *Linostylis ovata* Sond.

Decumbent to erect perennial herbs with cystoliths. Leaves opposite. Inflorescence of dichasia in leaf axils throughout plant or restricted to axils of distal leaves or bracts and forming a spike or thyrse; dichasia alternate or opposite, 1–many-flowered, sessile to pedunculate, subtended by a leaf or bract. Flowers homostylous, sessile to subsessile (in ours), subtended by 2 homomorphic bracteoles. Calyx 5-lobed, tube often as long as or longer than lobes during anthesis, regions between lobes usually subhyaline, often splitting nearly to base in fruit, lobes equal to subequal in length, usually somewhat setaceous. Corolla blue to blue-purple (in ours, elsewhere also pinkish purple, red, white, and yellow), tube gradually or abruptly expanded distally into a ± distinct throat, limb subactinomorphic to 2-labiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes contorted in bud. Stamens 4, didynamous, filaments connate in pairs (i.e., a long and a short stamen connate) proximally, exserted from mouth of corolla (at least longer pair and usually with at least a portion of anthers of shorter pair also), anthers 2-thecous, thecae equal in length, parallel to subsagittate, equally inserted, appendaged at base with awns or stout trichomes (in ours, elsewhere sometimes unappendaged at base), dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 12) subprolate to perprolate, 3-colporate, irregularly polypseudocolpate, pseudocolpi 4–12 per mesocolpium, exine minutely verrucate to microechinate (and often microfoveolate to microfossulate); staminodes 0. Style exserted from mouth of corolla, stigma unequally 2-lobed, 1 lobe greatly reduced, rudimentary, or sometimes not evident. Capsule substipitate, subellipsoid to ellipsoid, retinacula present, septae with attached retinacula remaining attached to inner wall of mature capsule. Seeds 2-4, homomorphic, lenticular, covered with appressed hygroscopic trichomes. (x = 15).

Dyschoriste consists of approximately 75 species occurring in tropical and warm-temperate regions of America, Africa, and Asia. The genus is best developed in the New World where it has a discontinuous distribution from the southern United States southward through Mexico and Central America to northern Argentina. Major concentrations of species are found in west-central and southern Mexico and southeastern Brazil. The actual number of Mexican species is likely fewer than the 22 presently recognized. *Dyschoriste* is a complex genus the described species of which offer few characters for their recognition. Kobuski's (1928) treatment of the American species is now outdated and inadequate both for delimiting and identifying taxa.

1. Herbage glandular or glands restricted to calyx, external surface of lower lip of corolla, and base of style. . . . . *D. hirsutissima*
1. Plants lacking glandular trichomes.
   2. Plants usually decumbent; stems puberulent with trichomes less than 0.05 to 0.2 mm long; calyx puberulent with mostly appressed trichomes 0.5–0.2 mm long; corolla 13–21 (–25) mm long; thecae (including basal appendage) 0.8–2 mm long. . . . . *D. decumbens*
   2. Plants mostly erect to diffuse; stems pubescent with at least some (usually all) trichomes 0.3–1.5 mm long; calyx pubescent with flexuose trichomes 0.5–2 mm long; corolla 20–29 mm long; thecae (including basal appendage) 2–2.6 mm long. . . . . *D. xylopoda*

Dyschoriste decumbens (A. Gray) Kuntze, Revis. Gen. Pl. 2:486. 1891. *Calophanes decumbens* A. Gray, Syn. Fl. N. Amer. 2(1):325. 1878. TYPE: MEXICO. Sonora: "near Santa Cruz, stony soil, in mountain valleys," 1851, *C. Wright 1462* (lectotype, designated by Henrickson, 1999: GH, photo at CAS!; isolectotypes: GH?, NY?).

Phenology. Flowering: March–September; fruiting: July–September.

Distribution and habitats. Southwestern United States (Arizona, New Mexico, Texas), Mexico (Baja California Sur, Chihuahua, Coahuila, Durango, Hidalgo, Querétaro, San Luis Potosí, Sonora, Zacatecas); Sonoran plants occur on rocky slopes in grasslands, oak woodlands, oak forests, and oak-pine forests at elevations from 1390 to 1800 m.

Illustrations. *Flora of Baja California*, 190. 1980; *Desert Plants* 5:169. 1984; *Proceedings of the California Academy of Sciences* 49:337. 1997.

In the protologue of *Calophanes decumbens*, Gray cited unspecified collections of Wright, Thurber, Rothrock, and others from western Texas, southern Arizona, and adjacent Mexico. Henrickson (1999) designated a specimen of *Wright 1462* at GH as the lectotype of that name. He further indicated that the lectotype was collected in the United States (Arizona). Whether the lectotype was collected in Arizona or Sonora (as treated here) depends on the date it was collected. It was undoubtedly collected in September of 1851 when Wright traveled through Santa Cruz Co., Arizona between Patagonia and Canelo Pass to Santa Cruz, Sonora (ca. 16 km S of the international border). Most of collections prior to 23 September were made in Arizona, those of 23 September were probably mostly made in Arizona, and those made from 24 September until 2 October were from Sonora (Shaw 1987). Shaw (1987) provided correlations between Wright's field numbers and localities, but there is no field number on either the lectotype or the isolectotype at GH. Nor are there any collections listed by Shaw (1987) in the field lists with the exact locality, habitat, and plant habit information as presented on the lectotype (see type citation above and habit described as "stems many, procumbent"). Based on the locality provided on the lectotype and localities in Wright's field lists (as provided by Shaw 1987), it seems more likely that this plant was collected in the grassland communities near Santa Cruz (in Sonora) rather than in similar habitats in nearby Arizona. Henrickson (1999) also noted that the number "1462" was assigned by Asa Gray to all of Wright's collections of this taxon, and that *Wright 1462* at MO from "valley of the Rio Grande" is therefore "not considered type material." However, Henrickson (1999) also indicated that *Wright 1462* at NY and another collection with this number at GH are isolectotypes. The label on these "isolectotype" specimens bear no locality data and therefore it remains a matter of speculation as to whether they represent type material or not.

Daniel (1984b, 1997) provided descriptions of this species. Henrickson (1999) treated *D. decumbens* as one of several varieties of a polymorphic *D. schiedeana* (Nees) Kuntze. He studied this difficult genus in considerable detail throughout north-central Mexico and the southwestern United States over many years. As a result, he is far more familiar with *Dyschoriste* in these regions than I am, and he is probably correct that *D. decumbens* is not deserving of specific rank. The problems for taxonomic delimitation that he noted (Henrickson 1999) are not restricted to the southwestern United States and northern Mexico, however. Study of plants occurring further to the south in Mexico reveals similar complexities involving these and other taxa (e.g., Daniel and Acosta 2003, cf. *D. microphylla* (Cav.) Kuntze), some of which have older names than *D. schiedeana*. Until such time as a satisfactory taxonomy has been promulgated for the genus throughout North America, I prefer to use traditionally recognized taxa with familiar names for regional treatments such as this one.

The leaves of *Van Devender et al. 98-882* vary from linear to narrowly elliptic (vs. elliptic to

oblanceolate to obovate in most other Sonoran collections of the species). This species is likely more common in the northern and eastern portions of Sonora than the relatively few known collections from the state (Fig. 14) would suggest.

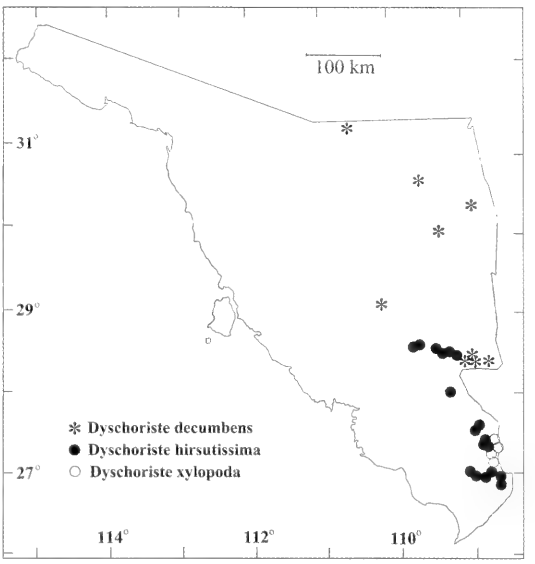


FIGURE 14. Sonoran distributions of *Dyschoriste decumbens*, *D. hirsutissima*, and *D. xylopoda*.

SONORAN COLLECTIONS: Yécora, 0.5 mi E of Arroyo Yécora, 28°23′N, 108°54′W, *M. Fishbein et al. 2487* (ARIZ); S of Pena Blanca on Hwy. 16, 28°23′N, 109°04′W, *P. Martin & G. Ferguson s.n.* (ARIZ); Mesa Grande, 28°26′N, 108°59′W, *P. Martin et al. s.n.* (ARIZ); Hwy. 16, 5.6 mi E of Río Maycoba, 6.5 mi W of Maycoba, 28°23′N, 108°43′W, *S. McMahon et al. 177* (ARIZ); Rancho La Pinosa, 5.9 mi W of Maycoba on Hwy. 16, 28°25′N, 108°43′W, *S. McMahon et al. 179* (ARIZ); "Sonora," *G. Thurber 114* (GH); Mpio. Yécora, 0.2 km N of Yécora on road to Agua Blanca, 28°23′N, 108°56′W, *W. Trauba s.n.* (CAS), *T. Van Devender et al. 97-786* (ARIZ, CAS); Mpio. Yécora, Rancho La Pinosa, 9 km E of Río Maycoba, 10.3 km W of Maycoba on Mex. 16, 28°25′N, 108°43′W, *T. Van Devender et al. 98-882* (CAS); Mpio. Santa Cruz, 3 km N of Santa Cruz on road to Nogales, 31°16′N, 110°36′W, *T. Van Devender et al. 2001-704* (CAS); Mpio. Ures, Cañada El Yugo, Sierra de Mazatan, 29°06′N, 110°12′W, *T. Van Devender et al. 2004-478* (CAS); KM 223, Rt. 69, 13 km NE of Guásabas, *T. Walker & S. Walker s.n.* (ARIZ); region of the Río de Bavispe, Horconcitos, Arroyo del Salto, *S. White 3761* (ARIZ); region of the Río de Bavispe, El Tajo, Río Fronteras, *S. White 4060* (ARIZ).

Dyschoriste hirsutissima (Nees) Kuntze, Revis. Gen. Pl. 2:486. 1891. *Calophanes hirsutissimus* Nees in A. de Candolle, Prodr. 11:109. 1847. TYPE: MEXICO. Hidalgo: "supra Hacienda de Guadalupe" [vicinity of Zacualtipán where Ehrenberg collected in November and December of 1839 fide Urban (1897)], Dec, *C. Ehrenberg 1223* (holotype: B, destroyed; fragment and photo: MO).

Calophanes bilabiatus Seem., Bot. Voy. *Herald*. 324. 1856. *Dyschoriste bilabiatus* (Seem.) Kuntze, Revis. Gen. Pl. 2:486. 1891. TYPE: MEXICO. Sinaloa: "Cerro de Pinal," Dec 1848, *B. Seemann 1513* (holotype: K!). "*Calophanes bilobatus* Rose" as treated in the synonymy of *D. hirsutissima* by Kobuski (1928), is treated as an orthographic error for *C. bilabiatus* because Rose (Contr. U.S. Natl. Herb: 1:109. 1891) cited the name as "Calophanes bilobatus Seem."

Ruellia viscosa Sessé & Moc., Pl. Nov. Hisp. 100. 1889, non *Ruellia viscosa* H.B.K. (1817). TYPE: not designated, see below.

Phenology. Flowering: March–July, October–December; fruiting: March–April, July, December.

Distribution and habitats. Mexico (Chiapas, Chihuahua, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Sinaloa, Sonora, Veracruz), El Salvador; Sonoran plants occur in thornscrub, tropical deciduous forests, oak grasslands, oak forests, and various riparian habitats at elevations from 220 to 1200 m.

Illustrations. *The Botany of the Voyage of H.M.S.* Herald, t. 65. 1856; *Flora del Valle de Tehuacán-Cuicatlán* 23:29. 1999.

Local names. "Ciática" (fide Van Devender et al. 2000); "valeriana del monte" (fide Van Devender et al. 2000).

Ruellia viscosa Sessé & Moc. is here treated as a synomym of *D. hirsutissima* for the first time. In the protologue of the former name, a locality is given as "in aridis Ayacapixtlae agris." According to McVaugh (2000) this is Yecapixtla, Morelos. In the Sessé and Mociño herbarium at MA no. *2156* (CNHM negs. 48997–48999) is labelled with this name and pertains to *Dyschoriste hirsutissima* (Nees) Kuntze. A painting in the Torner Collection (6331.0634) at the Hunt Institute for Botanical Documentation, Pittsburgh, U.S.A. is also labelled with this name and could represent *D. hirsutissima*. The description in the protologue, especially the foliar pubescence being "villoso-viscosa," would appear to pertain to this species as well.

Daniel (1995a, 1999a) and Daniel and Acosta (2003) provided descriptions of *Dyschoriste hirsutissima*. The vegetative organs of plants of this species are commonly viscid and have a somewhat mephitic odor (similar to that of *Ruellia inundata*). The species attains the northern and western extents of its distribution in southeastern Sonora (Fig. 14).

Sonoran collections: Mpio. San Javier, 2.7 km E of La Barranca on Mex. 16, 28°34′N, 109°40′W, *A. Búrquez M. 96-135* (CAS, MEXU); along Hwy. 16 between Tecoripa and Tónichi, 7.6 mi W of Río Yaqui, *T. Daniel 3344* (CAS); Mpio. Yécora, along Hwy. 16, 15.5 km NW of Tepoca, ca. 28°28′N, 109°21′W, *T. Daniel et al. 8559* (CAS); W of Alamos, *F. Drouet & D. Richards 3982* (CAS, DS, F, NY, US); 5.9 mi SE of San Bernardo on road up Arroyo Taymuco to mine at San Rafael, 27°21′N, 108°49′W, *M. Fishbein et al. 940* (ARIZ, CAS); Sierra de Alamos, Arroyo Uvalama, 27°00′N, 108°59′W, *M. Fishbein et al. 1098* (ARIZ); 8.2 mi S of Guajaráy on road to San Bernardo, 27°32′N, 108°56′W, *M. Fishbein et al. 1592* (ARIZ); KM 196 on Hwy. 16 W of Tepoca, *G. Ferguson & C. Moore s.n.* (ARIZ); Distr. Alamos, Qüiricoba, *H. Gentry 757* (DS), *757M* (F); Arroyo Gochico, Río Mayo, *H. Gentry 3634* (ARIZ, F, MEXU); Mpio. Alamos, Río Cuchujaqui near San Pedro, 27°02′N, 108°42′W, *P. Jenkins 89-427* (ARIZ), *89-428* (ARIZ); Sierra de Alamos, 27°54′N, 108°57′W, *P. Jenkins s.n.* (ARIZ); 20 mi E of Río Yaqui on Mex. Hwy. 16, *G. Joseph & B. Perrill 83-042* (ARIZ); Puenta La Pila above "El Palmar," ca. 20 km E of Onavas, 28°29′N, 109°22′W, *E. Joyal 1567* (CAS, MEXU); Arroyo Verde, *P. Martin s.n.* (ARIZ); 12 km E of Alamos, *P. Martin s.n.* (ARIZ, CAS); Río Yaqui drainage, Cerro Verde, 28°34′N, 109°44′W, *P. Martin & G. Ferguson s.n.* (ARIZ, CAS); above Rancho Palo Injerto, 27°03′N, 108°44′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); Río Cuchujaqui, between Rancho San Pedro and Cerro El Tarahumara, ca. 27°03′N, 108°42–43′W, *P. Martin et al. s.n.* (ARIZ); Jorinabo, 27°15′N, 108°46′W, *P. Martin et al. s.n.* (ARIZ); Alamos, *E. Palmer 402* (US); 18 mi SE of Río Yaqui on Mex. Hwy. 16, *R. Perrill 5322* (ARIZ); Mpio. Yécora, 3 km N of Tepoca on Mex. 16, 28°27′N, 109°16′W, *A. Reina G. & T. Van Devender 97-349* (CAS); Mpio. Alamos, Upper Río Cuchujaqui, Arroyo Verde, 27°06′N, 108°43′W, *R. Rondeau & G. Rodda 90-68* (ARIZ); Sierra de Alamos, vicinity of Alamos, *J. Rose et al. 12833* (US); 7 mi N of Güirocoba, 26°59′N, 108°41′W, *J. Salmon s.n.* (ARIZ); Sierra de la Cebollita, 6.4 mi S of Nuri along road from Tesopaco, ca. 28°04′N, 109°20′W, *A. Sanders 3689* (CAS); Mpio. Alamos, SW edge of Alamos in foothills of Sierra de Alamos, ca. 27°01′N, 108°57′W, *A. Sanders et al. 13359* (CAS, TEX); Mpio. Alamos, Cañón Los Laureles, E slope Sierra de Alamos, 108°58′W, 26°58′N, *A. Sanders et al. 14343* (CAS, MO); Arroyo Gochico, ca. 10 km E of San Bernardo, ca. 27°24′N, 108°44′W, *V. Steinmann et al. 605* (ARIZ, CAS, MEXU, NY); Sierra de Alamos, W of Aduana, ca. 6 km W of Alamos, 27°02′N, 109°01′W, *V. Steinman et al. 93-122* (ARIZ, MEXU); 21 mi E of Tónichi (at Río Yaqui) on road to Yécora, *L. Toolin 296* (ARIZ); Canyon las Piedras, Sierra de Alamos, 3.5 km S of Alamos, 26°59′N, 108°57′W, *T. Van Devender et al. 92-743* (ARIZ, CAS); El Guayabo crossing of Río Cuchujaqui, 14 km ESE of Alamos, 27°00′N, 108°47′W, *T. Van Devender et al. 93-170* (ARIZ); 4.5 km ESE of El Caracol on Alamos-Navojoa Road, 27°04′N, 109°02′W, *T. Van Devender et al. 93-225* (ARIZ, CAS, TEX); Rancho La Junta, 1 km upstream from Mesa Colorada, 3 km NNE of Burapaco, 27°35′N, 108°52′W, *T. Van Devender et al. 93-395* (ARIZ, CAS); near Tojibampo, 19.5 km NNW of San Bernardo on road to Mesa Colorado, 27°02′N, 108°47′W, *T. Van Devender et al. 93-1491* (ARIZ); Mpio. San Javier, 2.7 km E of La Barranca on Mex. 16, 28°34′N, 109°40′W, *T. Van Devender et al. 96-3* (ARIZ, CAS, MEXU, MO, NY, TEX); Mpio. Yécora, Agua Amarilla, 15 km WNW of Tepoca, ca. 28°08′N, 109°20′W, *T. Van Devender et al. 96-21* (ARIZ); 3 km E turnoff to Santa Ana on Mex. 16, 28°25′N,

109°07′W, *T. Van Devender et al. 97-248* (MEXU); Mpio. San Javier, Puerto San Juan, Cerro San Juan, near San Javier, 28°35′N, 109°45′W, *L. Varela E. 97-55* (CAS); San Javier, Cerro San Juan, 28°36′N, 109°45′W, *L. Varela & E. Cuamea 97-80* (MEXU); above Aduana, Sierra de Alamos, 7.5 km ESE of Alamos, 27°02′N, 109°01′W, *J. Wiens et al. 93-078* (ARIZ, CAS).

Dyschoriste xylopoda Kobuski, Ann. Missouri Bot. Gard. 15:54. 1928. TYPE: MEXICO. Jalisco: near Guadalajara, 19 Jul 1893, *C. Pringle 4442* (holotype: MO!; isotypes: F, GH!, MEXU!, MO!, PR!, PRC!, UC!, US!).

Erect to spreading (to decumbent) perennial herbs to 4 dm tall. Young stems subquadrate to quadrate-sulcate, ± evenly to ± bifariously pubescent with flexuose eglandular trichomes 0.2–2 mm long (sometimes with an understory of shorter, ± bifariously disposed, and antrorse trichomes as well). Leaves subsessile to short-petiolate, petioles to 2 mm long, blades linear to narrowly elliptic to elliptic to obovate, 10–36 mm long, 2–17 mm wide, 2.3–9 times longer than wide, rounded to acute at apex, acute to subattenuate at base, surfaces sparsely pubescent (sometimes nearly glabrous) with flexuose eglandular trichomes to 1.5 mm long, margin entire, ciliate (at least near base of blade) with similar trichomes. Inflorescence of dichasia borne in axils of leaves along distal portion of stems; dichasia opposite, 1 per axil, 1–many-flowered, pedunculate, peduncles 0.5–1.5 mm long. Bracteoles foliose, linear to narrowly elliptic to obovate, 8–21 mm long, 0.8–4 mm wide, sometimes slightly curved, abaxial surface pubescent like leaves, secondary bracteoles similar to bracteoles except often smaller. Flowers sessile to subsessile (i.e., pedicels to 1 mm long). Calyx 9.5–17 mm long, tube 3–7 mm long, .27–.44 times as long as calyx, lobes subulate-setaceous, 6.5–10 mm long, 1.3–2.7 times longer than tube, abaxially and marginally (at least near base) pubescent with flexuose eglandular trichomes (sometimes dense) 0.5–2 mm long. Corolla bluish-purple, 20–29 mm long, externally pubescent with flexuose eglandular trichomes 0.1–0.5 mm long, tube expanded just distal to midpoint, 15–19.5 mm long, 2.8–3 mm in diameter near midpoint, limb 15–20 mm in diameter, upper lip 7.5–9.5 mm long, lobes 4.5-6 mm long, 4–5.8 mm wide, lower lip 7.5–10 mm long, lobes 6–8.5 mm long, 4–6 mm wide. Stamens with longer pair 7–13 mm long, shorter pair 6–11.5 mm long, thecae parallel, 2–2.6 mm long (including basal appendage), awned at base, awn 0.2–0.3 mm long. Style 19–22 mm long, pubescent with eglandular trichomes, stigma 1.2–1.6 mm long, only 1 lobe evident. Capsule 8–10 mm long, glabrous.

Phenology. Flowering: July–September; fruiting: August–October.

Distribution and habitats. Western Mexico (Aguascalientes, Chihuahua, Durango, Jalisco, Nayarit, Sonora); Sonoran plants occur on slopes in oak woodlands and oak-pine woodlands at elevations from 900 to 1600 m.

Illustration. None found.

Sonoran plants resembling those of *Dyschoriste xylopoda* from the Nueva Galicia region to the south are treated as conspecific with them pending a satisfactory taxonomic treatment of the genus in North America. The species attains the northern and western extents of its distribution in the upper drainage of the Río Mayo in southern Sonora (Fig. 14). Most Sonoran plants are erect to spreading in habit. *Pennell 19615* is described as a "depressed herb" and looks to be spreading on the ground with upturned distal shoots. Thus, it has a habit similar to most plants of *D. decumbens*. The relationship of this species to that traditionally referred to *D. ovata* (Cav.) Kuntze (see discussion of this name in Daniel, 1995a) remains to be resolved.

Sonoran collections: ca. 35 km NE of Alamos, between El Chiribo and La Vinateria, 27°18′N, 108°42′W, *M. Fishbein et al. 1440* (ARIZ, CAS); 1 km E of Los Llanitos on road to Chiribo from Huicoche, 27°19′N, 108°39′W, *P. Martin & D. Yetman s.n.* (ARIZ); ridge S of Arroyo Gochico, E of San Bernardo, *F. Pennell 19540* (PH, US); Cerro Saguarivo, E of San Bernardo, *F. Pennell 19615* (PH, US); Rancho Santa

Bárbara, E of Alamos, 27°07′N, 108°43′W, *J. Rascon & C. Smith s.n.* (ARIZ); Sierra Sahuaribo, ca. 3 km N of La Lobera toward Huicochic, ca. 27°17′N, 108°37′W, *V. Steinmann et al. 93-237* (CAS).

Elytraria Michx.

Elytraria Michx., Fl. Bor.-Amer. 1:8. 1803, nom. cons. TYPE: *Elytraria virgata* Michx., nom. illegit. (= *Elytraria caroliniensis* (J.F. Gmel.) Pers.).

Tubiflora J.F. Gmel., Syst. Nat. 2:27. 1791, nom. rej. TYPE: *Tubiflora caroliniensis* J.F. Gmel.

Erect to ascending, acaulescent to caulescent perennial herbs lacking cystoliths. Leaves alternate, mostly in basal rosettes or crowded at apices of branches, sometimes ± diffuse along stems. Inflorescence of scapose or pedunculate densely bracteate axillary and terminal dichasiate spikes; spikes cylindric, simple or sometimes branched, scapes or peduncles covered with imbricate, coriaceous, clasping scales; dichasia alternate (spirally arranged), 1-flowered, sessile in axil of a bract. Flowers homostylous, sessile, subtended by 2 homomorphic (often mostly hyaline) bracteoles. Calyx deeply 4-lobed, mostly hyaline, lobes heteromorphic, anterior and posterior lobes external, anterior lobe 2-dentate to ± deeply 2-cleft. Corolla relatively small, pinkish or blue or white or yellow, often with colored markings, tube cylindric or slightly expanded near mouth, throat indistinct or evident only near mouth, limb 2-labiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes often apically divided or 2-cleft, imbricate in bud. Stamens 2, anthers partially exserted from mouth of corolla, 2-thecous, thecae (covered by stigma during anthesis) equal in size, parallel, equally inserted on filament, lacking basal appendages (at least in Mexican species), dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 12) euprolate to perprolate, 3-colpate, exine finely reticulate; staminodes 0–2, minute. Style exserted from mouth of corolla, stigma unlobed, expanded, flat, subelliptic to subspatulate, folded over anthers during anthesis and straightening when touched (touch-sensitive) and gradually refolding. Capsule estipitate, subconic to ovoid, sometimes irregularly constricted proximally, retinacula absent, placentae minute, papilliform. Seeds numerous (up to 20 per capsule), irregularly shaped (often blocky or cubelike), lacking trichomes. ($x = 11$ or 12?).

Elytraria consists of about 15 species occurring in the tropics and subtropics of both the Old World and the New World. The majority of species are American with four occurring in Mexico. Leonard's (1934) brief account of the American species is much out of date.

Elytraria imbricata (Vahl) Pers., Syn. Pl. 1:23. 1805. *Justicia imbricata* Vahl, Eclog. Amer. 1:1. 1796. TYPE: not located, see Daniel (1995a).

Verbena squamosa Jacq., Pl. Hort. Schoenbr. 1:3. 1797. *Tubiflora squamosa* (Jacq.) Kuntze, Revis. Gen. Pl. 2:500. 1891. *Elytraria squamosa* (Jacq.) Lindau, Anales Inst. Fís.-Geogr. Nac. Costa Rica 8:299. 1895. TYPE: unknown.

Elytraria tridentata Vahl, Enum. Pl. 1:107. 1804, nom. illegit. (*Justicia imbricata* Vahl cited as synonym).

See Daniel (1995a) for a complete listing of synonyms for this species.

Phenology. Flowering: August–May, but with peak flowering periods in March and September (Fig. 1); fruiting: throughout the year.

Distribution and habitats. Southwestern United States (Arizona, New Mexico, Texas), Mexico (Baja California Sur, Campeche, Chiapas, Chihuahua, Coahuila, Colima, Durango, Guanajuato, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, Sinaloa, Sonora, Veracruz, Yucatán, Zacatecas), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Ecuador, Peru, Bolivia, Brazil, Argentina, West Indies,

Old World (introduced); Sonoran plants occur on slopes, along watercourses, and in disturbed areas in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Plains of Sonora), thornscrub, grasslands, tropical deciduous forests, riparian forests, oak forests, oak-pine forests, and pine forests at elevations from sea level to 1680 m.

Illustrations. Figure 15; *Contributions from the United States National Herbarium* 31:91. 1951; *Fieldiana, Botany* 24(10):365. 1974; *Flora of Baja California*, 192. 1980; *Flora of the Venezuelan Guayana*, vol. 2, 347. 1995; *Flora of Chiapas* 4:38. 1995; *Proceedings of the California Academy of Sciences* 49:340. 1997; *Flora del Valle de Tehuacán-Cuicatlán* 23:35. 1999.

Local names. "Baiboria" (fide Gentry 1963); "cola alacrán" (*Felger & Yetman 97-132*); "cordoncillo" (Mexican, e.g., *Búrquez et al. 94-160*, *Felger & Yetman 96-193*, *Palmer 285*, *Pennington 258*, *White 2772*); "cordonsillo" (*Hartman 91*); "coronia" (*Gentry 1048*); "mahilí guasira" (Guarijío, *Felger & Yetman 96-193, 97-132*); "nachachíkoli" (Guarijío, *Gentry 1133*).

Uses. Used medicinally to treat scorpion sting (*Felger & Yetman 96-193*); tea made from root drunk three or more times per day for fevers or influenza (*Felger & Yetman 97-132*); herbage decocted or infused for fevers (*Gentry 1048, 1133*, and fide Gentry 1963 in reference to its use by the Guarijío); a medicinal tea (mix with mescal) made from plant taken for colds and fever (*Pennington 226*); remedy for fevers, venereal diseases, etc. (*Palmer 285*); a refreshing tea made from leaves (*Pennington 258*); a tea from the whole plant used to treat diarrhea and the leaves and inflorescence are boiled (often together with leaves of *Carlowrightia arizonica*) and taken as a tea for fever (including malarial fevers), according to Yetman and Van Devender (2002) in reference to its medicinal uses by the Mayo.

Daniel (1995a, 1997, 1999a) and Daniel and Acosta (2003) provided recent descriptions of this species in various regions of Mexico. *Elytraria imbricata* occurs in diverse communities (noted above) and is widespread in Sonora (Fig. 16). It occurs in three of the four subdivisions of the Sonoran Desert there, but appears to be absent from the Lower Colorado River Valley subdivision in northwestern Sonora. Plants are often leafless or nearly so during the dry season (e.g., January–May) when most flowering occurs; plants collected during the rainy season (e.g., August–September) are very leafy.

Sonoran collections: Río de los Alisos, ca. 6 mi N of Cumeral, *L. Abrams 13159* (DS); 1 mi N of Cumeral on Nogales road, *L. Abrams 13175* (DS, F); Nacopule Canyon, ca. 4 mi. N of San Carlos Bay, *M. Ames 77-67* (ARIZ); Río Cuchujaqui, near Alamos, *M. Ames 77-85* (ARIZ); Mpio. Opodepe, road to La Colmena Microwave Station at KM 76 N of Hermosillo, *B. Bartholomew et al. 2468* (CAS, GH, MEXU, MO, NY); Yaqui River, El Toledo, 28°34′N, 109°33.5′W, *G. Boyer et al. s.n.* (ARIZ); Guaymas, *T. Brandegee s.n.* (F); 2.5 km S de Hermosillo, 29°01′N, 110°57′W, *A. Búrquez & A. Quijada 91-21* (MEXU); El Himalaya (Peña Blanca), entre San Carlos y Tastiota, 28°11′N, 111°20′W, *A. Búrquez et al. 91-300* (MEXU); KM 295 carr. fed. 16, 2.5 km W de los Vallecitos, 28°23′N, 108°50.5′W, *A. Búrquez et al. 92-415* (MEXU); Cañón Tepoca, KM 177, Carr. Fed. 16, 28°27′N, 109°15′W, *A. Búrquez et al. 94-160* (MEXU); Cerro El Verde, San Javier, 28°33′N, 109°43′W, *A. Búrquez et al. 96-042* (MEXU); Mpio. Alamos, 53.9 km N of Alamos, 3.5 km NE of San Bernardo toward San Rafael, *C. Cowan et al. 5554* (TEX); between Cananea and Arizpe, 27.7 mi N crossing of Río Bacanuchi, ca. 30°50′N, 110°20′W, *T. Daniel 922* (CAS); between Tecoripa and Tónichi, 9.3 mi E of Tecoripa, *T. Daniel 982* (CAS); "Microondas Mountain" overlooking Guaymas, along road which is 1.8 mi from Mex. Hwy. 15 on paved road to airport, N of Guaymas, *T. Daniel 1953* (ASU); Nacapuli Canyon, 6.3 mi W of Hwy. 15 on road to San Carlos then 4.4 mi N, *T. Daniel 1986* (ASU); road between Hwy. 16 E of Tónichi and Onavas, 0.5 mi S jct. Hwy. 16, *T. Daniel 3351* (CAS); Río Cuchujaqui, 7.4 mi SE of Alamos toward Güirocoba, *T. Daniel 3383* (CAS), *4001* (CAS); southeastern border of Alamos (road to mirador), ca. lat. 27°01′N, long. 108°56′W, *T. Daniel 9770* (CAS); Mpio. Soyopa, crossing of Río Yaqui with Hwy. 16, 8.5 km W of jct. to Onavas, ca. 28°34′N, 109°33′W, *T. Daniel et al. 8512* (CAS, MEXU); Mpio. Yécora, between San Nicolás and Nuri, just S of Curea, ca. 24 km SW jct. Hwy. 16, ca. 28°19′N, 109°17′W, *T. Daniel et al. 8578* (CAS); W of Río Magdalena, Magdalena, *F. Drouet & D. Richards 3813* (DS, F); moun-

FIGURE 15. Sonoran Acanthaceae. a. *Holographis virgata*. b. *Holographis pallida*. c. *Pseuderanthemum praecox*. e. *Stenandrium pilosulum*. e. *Elytraria imbricata*.

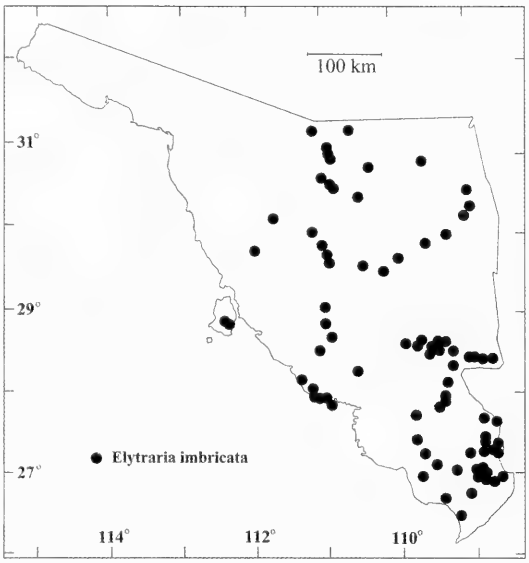


FIGURE 16. Sonoran distribution of *Elytraria imbricata*.

tain E of Guaymas, *F. Drouet & D. Richards 3843* (CAS, DS, F, MO, NY, US); 4 km NW of Alamos, *F. Drouet & D. Richards 4011* (F); El Cerro de la Campana, Hermosillo, *F. Drouet et al. 3388* (DS, F, GH, US); Rancho La Brisca, 3.5 mi. N of Agua Fria, 30°24′N, 110°33′W, *R. Duncan s.n.* (ARIZ); 6.3 mi. E of Río Bavispe on Guásabas-El Coyote Road, Cañón Cruz de Peñasco, *R. Felger 3645* (ARIZ); Nacapule Spring, NE of Bahía San Carlos, *R. Felger 4082* (ARIZ); 3 mi W of Nuri, *R. Felger 4096* (ARIZ); 0.8 mi S of Sabino, ca. 10 mi NE of Alamos, *R. Felger 5060* (ARIZ); Agua Caliente, 3.6 mi. S of La Casita on Mex. 15, *R. Felger 5629* (ARIZ, ENCB); E end of Bahía San Carlos, *R. Felger 6552* (ARIZ); Rancho San Jorge (W of Hermosillo), ca. 29°44′N, 111°51′W, *R. Felger 6907* (ARIZ); 14.7 mi. N of Imuris on Mex. 15, *R. Felger 7248* (ARIZ); Isla Tiburón, SE base of Sierra Kunkaak, *R. Felger 9315* (ARIZ, ENCB); Agua Caliente, *R. Felger 13989* (ARIZ, UC); ca. 1 km N of Bahía San Carlos toward Bahía Algadones, *R. Felger & R. Devine 85-3301* (ARIZ); Cañón Nacapuli, ca. 4 km N of Bahía San Carlos, *R. Felger & M. Dimmitt 85-862* (ARIZ, CAS); 10.2 mi. S of La Pintada (between Hermosillo and Guaymas) on Mex. 15, *R. Felger & C. Lowe 8365* (ARIZ); Cerro de la Vigia, Guaymas, *R. Felger & R. Thomas 11832* (ARIZ); Cañón Nacapule, NE of Bahía San Carlos, *R. Felger & R. Thomas 11861* (ARIZ, ENCB), *12002* (ARIZ); Mpio. Alamos, Río Mayo drainage, ca. 16 km N of Mesa Colorado, ca. 27°42′N, 108°50′W, *R. Felger & D. Yetman 96-193* (ARIZ, CAS); Mpio. Alamos, ca. 3 km SE of Bavícora, 27°40′N, 108°47′W, *R. Felger & D. Yetman 97-132* (CAS); Cañón Nacapules, ca. 6 km NE of Bahía San Carlos, *R. Felger et al. 84-120* (ARIZ); 0.5 mi SE of Alamos at jct. Güirocoba and El Fuerte rds., *J. Fish 44* (UC); S of Los Molinos, 7.8 mi. N of Los Tanques on road from Alamos to San Bernardo, 27°18.5′N, 108°53′W, *M. Fishbein et al. 930* (ARIZ); Mpio. La Colorada, 2.5 km S de El Pilar, 28°39′N, 110°52′W, *A. Flores M. & J. León G. 5396* (IEB); Distr. Alamos, Qüirocoba, *H. Gentry 760* (DS, US); Canyon Sapopa, Río Mayo, *H. Gentry 1048* (F, GH, MO, S, WIS); Conejos, Río Mayo, *H. Gentry 1133* (F); Guaymas, *H. Gentry 4697* (ARIZ); Sierra Bojihuacame SE of Cd. Obregón, *H. Gentry 14494* (ARIZ, MEXU, LL, US); 4.3 km SW of Santa Ana de Yécora on road to Nuri, 28°23′N, 109°19′W, *D. Goldberg & S. McLaughlin 77-165* (ARIZ); ca. 30 mi S of Hermosillo on Hwy. 15, *B. Hansen et al. 1380* (LL, MEXU, US, WIS); Cochuto, *C. Hartman 91* (GH, NY, PH, US); Calabasas, *C. Hartman 109* (F, GH); Río El Naranjo crossing, N of Taymuco, 27°15′N, 108°43′W, *P. Jenkins 88-175* (ARIZ); Guaymas, *I. Johnston 3092* (CAS); San Carlos Bay, *I. Johnston 4389* (CAS); Hermosillo, *M. Jones 22576* (MEXU, MO, PH); Las Cabras, ESE of Alamos, 27°00′N, 108°55′W, *E. Joyal 1422B* (CAS); Rancho El Aguilar Noria, N of Ures and Santiago, 29°33′N, 110°25–26′W, *E. Joyal 1819* (MEXU); Tiburón Island, Sierra Kunkook, *Knight 1016* (UNM); Tiburón Island, San Miguel Peak, *Knight et al. 961* (UNM); ca. 70 mi S of Hermosillo, *G. Lindsay 1137* (DS); Salsipuede, *C. Lloyd 442* (GH); Palm Canyon, 18 mi. SE of Magdalena, *P. Martin s.n.* (ARIZ); 5 km N of Rosario de Tesopaco, *P. Martin s.n.* (ARIZ); Mocúzari, La Cruz, 27°13′N, 109°05.5′W, *P. Martin s.n.* (ARIZ); La Fundición camp., road to San Pedro, 27°06′N, 108°45.5′W, *P. Martin & G. Ferguson s.n.* (ARIZ); Cerro Verde, 28°34′N, 109°44′W, *P. Martin & G. Ferguson s.n.* (ARIZ); 3 km S of Santini, KM 175 on Obregón-Navojoa road, 27°16′N, 109°39′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); 1 km NE of Bachoco, *P. Martin & M. O'Rourke s.n.* (ARIZ); 1 km E of El Chiribo, 27°18′N, 108°42′W, *P. Martin & D. Yetman s.n.* (ARIZ); Yaqui River, El Toledo, 28°34′N, 109°34′W, *P. Martin et al. s.n.* (MO, US); Estación Margarita, 10 km NW of Navojoa, 27°08.5′N, 109°29′W, *P. Martin et al. s.n.* (ARIZ); Arroyo Santa Rosa, 10 km NE of Tesopaco, 27°56′N, 109°19′W, *P. Martin et al. s.n.* (ARIZ); Canyon de las Palmas, Sierra Baviso, 16 mi SE of Magdalena, *N. McCarten 2264* (ENCB); Cañón Los Anegados, Sierra El Aguaje, Ejido Francisco Villa, 28°02′N, 111°08′W,

Moreno L. et al. 99-25 (ARIZ); Alamos District, near Minas Nuevas, *R. Moran 4030* (DS, UC); Guaymas, *E. Palmer 285* (C, GH, NY, US); without locale, *E. Palmer 12691* (MO), *s.n.* [in 1869] (PH, US); Maicoba, *C. Pennington 226* (TEX); Onavas, *C. Pennington 258* (TEX); 2.5 mi. W and 0.75 mi S of Alamos, *R. Perrill & V. Phelps 5167* (ARIZ); Nacopuli Canyon, 3.5 mi. N of San Carlos Bay, *A. Phillips et al. 75-158* (ARIZ); 8 mi E of Moctezuma on Huásabas Road, 29°50′N, 109°23′W, *F. Reichenbacher 188* (ARIZ); Mpio. Guaymas, old road to Algodones, San Carlos, 27°58′N, 111°04′W, *A. Reina G. & T. Van Devender 2000-916* (CAS); Guaymas, *J. Rose 1275* (US); vicinity of Guaymas, *J. Rose et al. 12588* (NY, US); vicinity of Alamos, *J. Rose et al. 12726* (NY, US); vicinity of Puerta de Mano, 26°59′N, 108°39′W, *J. Salmon s.n.* (ARIZ); 10 mi N of San Carlos, "Catch-22" site, *D. Shaw 29* (MO); Mpio. Villa Pesqueira, Sierra Pinta, ca. 33 mi. S of Moctezuma, ca. 29°35′N, 110°01′W, *J. Shortman & M. Wilson 96-58* (ARIZ); 37 mi. NE of Cajeme on road to Tesopaco, *F. Shreve 6155* (ARIZ); Sierra Baviso, 19 mi E of Magdalena, *F. Shreve 6642* (F, GH, MO); 7 mi S of Estación Carbo, *F. Shreve 6688* (GH); 25 mi. E of La Motica on road to Tezopaco, *W. Spaulding 75-3-17* (ARIZ); ca. 10 mi W of Tezopaco toward Cd. Obregón, *W. Spaulding 75-3-36* (ARIZ); 2.6 mi. ESE of Alamos toward Río Cuchujaqui crossing at Sabinito Sur, Cerro Las Campas, 27°01′N, 108°54′W, *G. Starr & D. Palzkill 335* (ARIZ); Mpio. Alamos, Sierra de Alamos, ca. 6 km W of Alamos, ca. 27°02.5′N, 109°01′W, *V. Steinmann & C. Smith 93-123* (ARIZ); along road between Yepachic and Yécora, 19 mi W of Chihuahua border, *S. Sundberg & M. Lavin 2837* (MO); Cerro Prieto Microondas, 15 km E de Navojoa, *P. Tenorio et al. 10185* (MEXU); Santa Cruz, *G. Thurber 950* (F); 4 mi. S of Mazocahui, *R. Turner 59-69* (ARIZ); 7.4 mi N of Las Chinacas, 27°18′N, 108°37′W, *R. Turner & P. Martin 79-396* (ARIZ); Bahía San Pedro, ca. 28.1°N, 111.2°W, *R. Turner et al. 79-258* (ARIZ); Güirocoba crossing of Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56′N, 108°53′W, *T. Van Devender et al. 92-903A* (ARIZ); Camahuiroa between Agiabampo and Las Cocas on Gulf of California, 26°31′N, 109°16′W, *T. Van Devender et al. 92-1084* (ARIZ, CAS); Mpio. Alamos, 1 km S of Yocogigua, 26°47′N, 109°02′W, *T. Van Devender et al. 93-1091* (ARIZ); Saucito Canyon, Rancho la Sierrita, E slopes of Sierra de Alamos, ca. 6 km SSW of Alamos, 26°58′N, 108°58′W, *T. Van Devender et al. 93-1333* (CAS); Mpio. Yécora, 5.3 km W of Yécora on Mex. 16, 28°22′N, 108°59′W, *T. Van Devender et al. 96-64* (ARIZ, MEXU); Mpio. Soyopa, near Arroyo Garambullo on NE side of Río Yaqui bridge on Mex. 16, just S of Tónichi, ca. 28°34′N, 109°33′W, *T. Van Devender et al. 98-1119* (NY, TEX); Mpio. Nogales, 1.3 km SE of Rancho Las Borregas headquarters on road to Nogales, 31°12′N, 111°07′W, *T. Van Devender et al. 2004-248* (CAS); Palm Canyon, 17.7 mi SE of Magdalena in Cerro Cinta de Plata, *T. Van Devender et al. s.n.* (ARIZ); San Javier, cañón lo de Campa entre los cerros El Potrerito y Los Amoles a 7 km S del poblado, 28°32′N, 109°45′W, *L. Varela E. 96-443* (MEXU); San Javier, Cerro San Juan, 28°36′N, 109°45′W, *L. Varela & E. Cuamea 97-66* (MEXU); Alamos, *F. Vilas 69-VII* (WIS); N of Guaymas, *U. Waterfall 12848* (F, SMU); 2 mi S of El Coyote, ca. 29°56′N, 109°08′W, *G. Webster & R. Murphey 21349* (ARIZ); Mpio. Yécora, ca. 2 km NW of Yécora toward Santa Rosa, 28°23′N, 108°51′W, *J. Weins et al. 96-107* (ARIZ); loop of the Río Bavispe, Cañón de Huépari, N of Aribabi, *S. White 2649* (ARIZ, GH); loop of the Río Bavispe, Puerto de Huépari, NW of Aribabi, *S. White 2772* (DS, MEXU); Bavispe, *S. White 2863* (GH); Horconcitos, Arroyo del Salto, *S. White 3774* (GH); 100 mi. from Magdalena, *J. Whitehead M127* (ARIZ); 4 mi N of Nuri, 28°10′N, 109°11′W, *A. Whittemore et al. 83-084* (MEXU, TEX); 2 mi E of Rancho San Carlos on road to Noria, *I. Wiggins 6146* (DS, US); Río Sásabe, 10 mi E of Magdalena, *I. Wiggins 7106* (DS, US); 10 mi N of Carbo, *I. Wiggins 7265* (DS, GH, UC, US); 1 mi E of RR on road from Carbo to Horcasitas, *I. Wiggins 7277* (DS, F, GH, LL, MO, UC, US); Sahuaribo (108°40′W, 27°20′N) to Corogui (108°41.5′W, 27°22′N), *D. Yetman et al. s.n.* (ARIZ).

Henyra Nees ex Benth.

Henrya Nees ex Benth., Bot. Voy. *Sulphur*, t. 49. 1845. TYPE: *Henrya insularis* Nees ex Benth.

Solenoruellia Baill., Hist. Pl. 10:445. 1891. TYPE: *Solenoruellia galeottiana* Baill. (= *Henrya insularis* Nees ex Benth.).

Baillonacanthus Kuntze in Post and Kuntze, Lex. Gen. Phan. 58. 1903 ("1904"). TYPE: *Solenoruellia galeottiana* Baill. (= *Henrya insularis* Nees ex Benth.).

Erect or ascending perennial herbs or shrubs with cystoliths. Leaves opposite. Inflorescences

of axillary and terminal stout to lax dichasiate spikes (to thyrses) collectively forming leafy terminal panicles; dichasia alternate or opposite, 1–3-flowered, sessile or short-pedunculate in axils of bracts. Flowers homostylous, sessile, subtended by 2 homomorphic bracteoles, bracteoles oblanceolate to obovate, usually larger and more conspicuous than bracts, concavoconvex, fused from base to near apex along side adjacent to rachis, rounded to acute at apex, mucronate with straight, apical or dorsal, erect or divergent pointed projection, secondary bracteoles, if present, much reduced. Calyx deeply 5-lobed, lobes homomorphic or heteromorphic (i.e., posterior lobe reduced in size). Corolla white, cream, or yellow, with maroon, purple, yellow, and/or white markings on upper lip, tube subcylindric to cylindric, throat indistinct, limb pseudopapilionaceous, upper lip comprising 2 fused lobes, 2-fid at apex, lower lip 3-lobed, lateral lobes similar to one another, lower-central lobe usually larger and keeled, corolla lobes imbricate in bud. Stamens 2, anthers 2-thecous, thecae subequal, parallel, equally to subequally inserted on filament, lacking basal appendages, dehiscing toward upper lip (i.e., flower stenotribal); pollen (Fig. 12) euprolate to perprolate, 3-colporate, colpi broad (i.e., far exceeding width of centrally positioned ora), 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine reticulate to bireticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed, lobes equal and often inconspicuous. Capsule stipitate, head subspheric to broadly ellipsoidal, retinacula present, septae with attached retinacula separating slightly from inner wall of mature capsule. Seeds 2, homomorphic, planoconvex, subcircular to subelliptic in outline, flat surface smooth to bumpy, convex surface and margin either pubescent with hygroscopic trichomes or covered with stout, branched or barbed tubercles. ($x = 18$).

Daniel (1990) treated *Henrya* as consisting of two species occurring in dry regions from the southwestern United States southward to Costa Rica. Both species occur in Mexico.

Henrya insularis Nees ex Benth., Bot. Voy. *Sulphur*, t. 49. 1845. TYPE: plate 49 of Bentham's *The Botany of the Voyage of H.M.S.* Sulphur, see Daniel (Taxon 38:265-270. 1989.)

Henrya costata A. Gray, Proc. Amer. Acad. Arts 21:406. 1886. *Tetramerium costatum* (A. Gray) Millsp., Publ. Field Columbian Mus., Bot. Ser. 1:47. 1895. TYPE: MEXICO. Chihuahua: near Batopilas, Aug-Nov 1885, *E. Palmer 211* (holotype: GH!; isotypes: K!, LE!, MEXU!, NY!, PH!, US!).

Henrya grandifolia Fernald, Bot. Gaz. (Crawfordsville) 20:537. 1895. TYPE: MEXICO. Sinaloa: Esquinapa, Jan 1895, *F. Lamb 505* (holotype: GH!).

Henrya costata A. Gray var. *glandulosa* Brandegee, Zoe 5:171. 1903. TYPE: MEXICO. Baja California Sur: Cape Region, Santa Anita, 1901, *C. Purpus 266* (lectotype, designated by Daniel, 1990: UC!; isolectotypes: ARIZ!, MO!, US!).

Henrya brevifolia Happ, Ann. Missouri Bot. Gard. 24:547. 1937. TYPE: MEXICO. Sonora: Las Durasnillas, 18 May 1892, *T. Brandegee s.n.* (holotype: UC!; isotypes: DS!, GH!, NY!, PH!, US!).

Henrya ortegana Happ, Ann. Missouri Bot. Gard. 24:552. 1937. TYPE: MEXICO. Sinaloa: Sind. San Juan, San Ignacio, Mar 1931, *J. Ortega 6868* (holotype: MO!; isotypes: CAS!, F!, MIN!).

See Daniel (1995a) for a complete listing of synonyms for this species.

Phenology. Flowering: January–June; fruiting: March–June.

Distribution and habitats. Southwestern United States (Arizona), Mexico (Aguascalientes, Baja California Sur, Chiapas, Chihuahua, Colima, Durango, Guanajuato, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Yucatán, Zacatecas), Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica; Sonoran Plants occur along watercourses and on rocky slopes in thornscrub, tropical

deciduous forests, oak woodlands, and oak-pine woodlands at elevations from 200 to 1380 m.

Illustrations. Figure 9; *Botany of the Voyage of H.M.S.* Sulphur, t. 49. 1845; *Flora of Baja California*, 193. 1980; *Flora of Chiapas* 4:40. 1995; *Proceedings of the California Academy of Sciences* 49:345. 1997; *Flora del Valle de Tehuacán-Cuicatlán* 23:41. 1999; *Flora del Bajio* 117:56. 2003.

Local names. "Alfalfillo" (fide Van Devender et al. 2000); "hegregado" (*Joyal 1563*); "rama del toro" (*Búrquez & Steinmann 96-110*, *Joyal et al. 1627*, *Van Devender et al. 93-1523*, *94-220*).

Brandegee (1893:347) indicated that "Las Durasnillas," the type locality of *Henrya brevifolia*, is "a small collection of houses about sixty miles from Hermosillo, near a mountain range known as Sierra Matapan." I did not encounter these place names on the series of maps available to me. A "Rancho Duraznillas" is located at 28°15′N latitude and 109°46′W longitude (Anonymous 1992), near the railroad between Est. Corral (near Esperanza) and Tónichi. *Henrya insularis* has been collected in this region, and there is a "La Dura" on most maps near these coordinates. This locality is nearly 100 miles from Hermosillo, however. The American Geographical Society's (1937) map of this region shows a "Duraznillo" about 60 miles east of Hermosillo along the road to Mazatan (at about 29°02′N, 110°17′W). There is a Río Mátape and a Sierra Mazatan in the general vicinity. This latter locality would have been more accessible to Brandegee from Hermosillo and it is presumed to be the type locality for both *H. brevifolia* and *Tetramerium abditum*. This locale is well within the range of *H. insularis* and *T. abditum* has been collected nearby.

Daniel (1990, 1995a, 1997, 1999a) and Daniel and Acosta (2003) provided descriptions of *Henrya insularis* and discussed regional morphological variation throughout its range. Plants from Sonora represent a common and widespread (Arizona to Central America) form of the species with bracts shorter than the bracteoles and the bracteolar mucros apically situated. Vegetative pubescence of Sonoran plants consists of an understory of eglandular (and usually glandular as well) trichomes and an overstory of glandular trichomes. Most Sonoran collections are noted to have yellowish corollas, usually with maroon or reddish markings on the upper lip.

The species is widely distributed in Sonora (Fig. 17) and occurs in diverse habitats. It likely also enters the Arizona Upland subdivision of the Sonoran Desert along the Río Magdalena near Magdalena. Its northernmost known occurrence is in the lower reaches of Sycamore Canyon in the Parajito Mountains along the Arizona-Sonora border, west of Nogales.

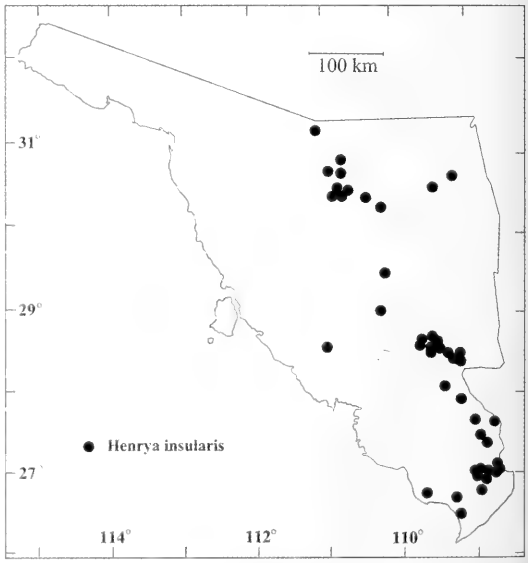


FIGURE 17. Sonoran distribution of *Henrya insularis*.

SONORAN COLLECTIONS: El Rancheria crossing of Río Cuchujaqui, ca. 22.5 km S of Alamos on road to El Chinal, 26°51′N, 108°55′W, *M. Baker et al. 10373* (TEX); Toro Muerto Canyon, ca. 2.5 mi W of Toro Muerto bridge on Hwy. 118, *J. Bowers et al. 2813* (ARIZ, ENCB); San Javier, 1 km de la Carr. Fed. 16, 28°35′N, 109°45′W, *A. Búrquez 93-121* (MEXU); San Javier, microondas en el Cerro El Durazno, 28°37′N, 109°45′W, *A. Búrquez 94-018* (MEXU); 0.5 km NW del Rancho Lo de Campa, San Javier, 28°34′N, 109°44.5′W, *A. Búrquez & V. Steinmann 96-110* (MEXU); Mpio. Huatabampo, Bocarehui [26°49′N, 109°43′W], *M. Cordova & R. Alcaraz s.n.* (ENCB); along road between Hwy. 16 E of Tonichi and Onavas, 0.5 mi S jct. Hwy. 16, *T. Daniel 3352* (CAS); along road between Rosario de Tezopaco and Nuri, 7.1 mi S of

turnoff to Nuri, *T. Daniel 3363* (ASU, CAS); Arroyo Cuchujaqui, 7.4 mi SE of Alamos toward Guiricoba, *T. Daniel 3377* (CAS); Mpio. Yécora, between San Nicolás and Nurí, ca. 6.4 km SW jct. Hwy. 16, ca. 28°24′N, 109°14′W, *T. Daniel et al. 8571* (CAS, MEXU); near Rancho La Brisca, ca. 8 mi ENE of Cucurpe, *J. Duek s.n.* (MEXU); Mpio. Guaymas, Sierra Libre, Cañón Tetabejo, 28°32′N, 110°59′W, *R. Felger et al. 02-297* (CAS); 9 mi from Imuris in Magdalena River canyon, *R. Ferris 8783* (DS, US); 6.3 mi NW of San Bernardo toward Guajaráy, 27°26′N, 108°57′W, *M. Fishbein et al. 1546* (ARIZ, CAS); Jopopaco vicinity, 2.2 km NE of Mex. 15 to Jopopaco, 25 km NW of Melchor Ocampo, 26°44′N, 109°16′W, *S. Friedman & O. Kiser 242-95* (ARIZ); Arroyo Camahuiroa, 1.5 km NE of Camahuiroa, 9.5 km WNW of Melchor Ocampo, 26°33′N, 109°16′W, *S. Friedman et al. 172-94* (ARIZ); Mpio. Imuris, 1.5 km W and 8 km S of Microondas Las Aguilas, Sierra de La Madera (E of Imuris), 30°40′N, 110°46.5′W, *G. Ferguson et al. 2338* (CAS); 21.5 mi E of Tecoripa, *P. Gallagher et al. 290* (ASU); 16.2 mi E of turnoff to Tonichi and 11.2 mi W of Tepoca along Mex. Hwy. 16, *P. Gallagher et al. 294* (ASU, CAS, NY); Alamos, Río Fuerte, *H. Gentry 2200* (ARIZ, F, GH, K, MEXU, MO, S, UC, US); Rancho Agrimincor, Río Mayo, *H. Gentry 3043* (ARIZ, F, GH, K, MEXU, MO, S, UC, US); Curohui, Río Mayo, *H. Gentry 3639* (ARIZ, F); Distr. Alamos, *H. Gentry s.n.* (MICH); 3.7 mi W of Santa Ana on old road to Yécora, *D. Goldberg 76-99* (ARIZ); Río Cuchujaqui, ca. 5 mi ESE of Alamos, 26°56′N, 108°53′W, *D. Goldberg & T. Van Devender 76-45* (ARIZ); Mpio. Alamos, cajón of the Río Cuchujaqui, 27°02–03′N, 108°42–42.5′W, *P. Jenkins 89-432* (ARIZ), *89-440* (ARIZ); Mpio. Alamos, Río Cuchujaqui, Guirocoba crossing 5 mi SE of Alamos, *P. Jenkins et al. 97-01* (ARIZ, CAS); Puente La Pila, ca. 20 km E of Onavas, 28°29′N, 109°22′W, *E. Joyal 1563* (CAS, MEXU); Río Cuchahaqui, SSE of Alamos, 26°52′N, 108°55′W, *E. Joyal et al. 1627* (MEXU); 7.5 mi W of Alamos, *R. Krizman 2* (ARIZ); ca. 4 mi NE of Santa Rosa on road to Yécora, *E. Lehto & T. Reeves L18746* (ASU); Rancho La Brisca, ca. 4-5 km N of Rancho Agua Fria on Río Santo Domingo, 30°24′N, 110°33′W, *P. Martin s.n.* (ARIZ, ENCB); 5 km SW of Santa Barbara, El Palmarito Canyon, 27°05′N, 108°45′W, *P. Martin & G. Ferguson s.n.* (ARIZ, CAS); Ignimbrite Canyon, 3 km N of La Brisca, Río Santo Domingo, 30°25′N, 110°53′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); Microondas Masiaca, 7 km W of Masiaca, 26°46.5′N, 109°18′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); above Las Animas, 27°31.5′N, 108°42′W, *P. Martin et al. s.n.* (ARIZ); Palm Canyon, 19 mi E of Magdalena, *C. Mason et al. 3294* (ARIZ, MEXU); Mpio. Alamos, Arroyo Santa Barbara, 27°07′N, 108°43′W, *S. Mathes & P. Martin s.n.* (ARIZ); 1.3 mi S of Cucurpe, *L. McGill & D. Pinkava 6491* (ASU, F); 2 mi N of Nuri, *S. McLaughlin 512* (ARIZ); 21 mi NE of Río Yaqui crossing on Mex. 16, *R. Perrill 5317* (ARIZ); Onavas, NW of pueblo, ca. 28°28′N, 109°32′W, *A. Rea 1052* (ARIZ); Rancho El Palmar, 22.6 km SE of Río Yaqui on Mex. 16, 28°30′N, 109°24′W, *A. Reina G. et al. 97-104* (MEXU); Mpio. Onavas, 4 km W of Agua Amarilla, 18.9 km W of Tepoca on Mex. 16, 28°29′N, 109°22′W, *A. Reina G. et al. 98-603* (CAS); Cerro Redondo, 27°05′N, 108°45′W, *R. Rondeau & G. Rodda s.n.* (ARIZ); Sierra de Alamos, *J. Rose et al. 12829* (NY, US); Río Cuchujaqui, ca. 7 mi ESE of Alamos, ca. 26°59′N, 108°50′W, *A. Sanders et al. 2573* (ARIZ, ASU, RSA); NW side of Sierra de Alamos along road from Alamos–Navojoa road at Rancho Las Lomas to Promontorios, *A. Sanders et al. 2613* (ASU); Sierra Madre Occidental, at three-way jct., 6 mi E of Tepoca, *A. Sanders et al. 2668* (ASU); Río Chico, 2 mi N of Nuri, *W. Spaulding 75-3-22* (ARIZ); Las Piedras Canyon, E side of Sierra Alamos, 26°59′N, 108°57.5′W, *G. Starr & D. Palzkill 363* (ARIZ); 1.8 mi N of Alamos on Cerro Dos Negritos, *G. Starr & D. Palzkill 368* (ARIZ); 20-25 mi NE of Ures, *R. Straw 2118* (RSA, UC); Cucurpe, near Río Dolores, *R. Thompson & O. Davis 82-46* (ARIZ); 21 mi E of Tonichi on Río Yaqui, *L. Toolin 297* (ARIZ); Río Cuchujaqui at Rancho El Conejo, 12.4 km S of Alamos, 26°55′N, 108°55′W, *T. Van Devender 92-561* (ARIZ); Mpio. Santa Ana, Canada El Rincon del Diablo, W slope of Sierra Cucurpe, ca. 13 km W of Cucurpe, 30°20′N, 110°51′W, *T. Van Devender & A. Reina G. 98-446* (CAS); Cañón de la Bota, N end of Sierra el Tigre, ca. 34 km ESE of Esqueda, *T. Van Devender et al. 82-61* (ARIZ); near crossing of Río Cuchujaqui ca. 8 mi SE of Alamos, *T. Van Devender et al. 84-146* (ARIZ); canyon N of Los Aguaros on Arroyo Guajaray, 27°38.5′N, 108°58′W, *T. Van Devender et al. 93-485* (ARIZ); El Rincon Viejo, ca. 4 km N of Alamos, Sierra de Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 93-1523* (ARIZ); Cerro Piedra Boluda, ca. 1 km NE of El Rincon Viejo, ca. 4.5 km N of Alamos, *T. Van Devender et al. 94-220* (ARIZ, CAS); Mpio. Yécora, Agua Amarilla (Los Pinitos), 15 km WNW of Tepoca, 24.7 km WNW of San Nicolas on Mex. 16 at KM 200, ca. 28°08′N, 109°20′W, *T. Van Devender et al. 96-23* (ARIZ); 1.5 km SW of Santa Ana on road to Guadalupe Tayopa, 28°23′N, 109°09′W, *T. Van Devender et al. 97-201* (MEXU, MO, TEX); 2.7 mi WNW of Tepoca on Mex. 16, ca. 28°28′N, 109°16′W, *T. Van Devender et al. 99-71* (NY); Mpio. Nogales, Sierra Las

Avispas, 15.9 km W of MEX 15 on SON 43 (to Sáric), 31°04′N, 111°05′E, *T. Van Devender et al. 2002-757* (CAS); Mpio. Nogales, 3.8 km NE of El Correo (La Arizona), Rancho Las Borregas, Arroyo Planchas de Plata, 31°11.5′N, 111°10′W, *T. Van Devender et al. 2004-217* (CAS); ca. 17 mi SSE of Magdalena, Cerro Cinta de Plata (=Sierra Babiso), *T. Van Devender et al. s.n.* (ARIZ, NY); Río Saracachi, ca. 5 mi NE of Cucurpe, *T. Van Devender et al. s.n.* (ARIZ); San Javier, Cerro San Juan, 28°36′N, 109°45′W, *L. Varela & E. Cuamea 97-68* (MEXU), *L. Varela & A. Feliz 97-34* (MEXU); Los Banos near Angostura, *S. Walker BAN 7* (NY); 13 mi E of Imuris, *I. Wiggins 11665* (DS, MEXU, MICH, TEX, UC, US).

Holographis Nees

Holographis Nees in A. de Candolle, Prodr. 11:728. 1847. TYPE: *Holographis ehrenbergiana* Nees.

Berginia Harv. ex Benth. & Hook.f., Gen. Pl. 2:1096. 1876. TYPE: *Berginia virgata* Harv. ex Benth. & Hook.f. (≡ *Holographis virgata* (Harv. ex Benth. & Hook.f.) T.F. Daniel).

Pringleophytum A. Gray, Proc. Amer. Acad. Arts 20:292. 1885. TYPE: *Pringleophytum lanceolatum* A. Gray. (= *Holographis virgata* (Harv. ex Benth. & Hook.f.) T.F. Daniel).

Lundellia Leonard, Wrightia 2:1. 1959. TYPE: *Lundellia argyrea* Leonard (≡ *Holographis argyrea* (Leonard) T.F. Daniel).

Erect to ascending perennial herbs or shrubs lacking cystoliths. Leaves opposite (rarely subopposite) or quaternate. Inflorescence of axillary or terminal dichasiate spikes (reduced to 2 flowers in *H. ehrenbergiana*); dichasia opposite to alternate, 1-flowered, sessile in axil of a bract. Flowers homostylous, sessile, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic. Corolla greenish white, white, pinkish to purplish, or yellow, often with colored nectar guides, long axis horizontally to vertically oriented, tube subcylindric to ± abruptly expanded distally into a throat, limb 2-labiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes imbricate in bud. Stamens 4, equally inserted to ± didynamous, anthers slightly exserted from mouth of corolla, anthers 1-thecous, often connivent, pubescent, lacking basal appendages, dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 18) euprolate to perprolate, 3-colpate, colpi often bifurcate near poles, exine psilate to verrucate to foveolate to rugulate; staminode 1, borne between posterior pair of stamens, short. Style slightly exserted from mouth of corolla, stigma subfunnelform or 2-lobed, lobes equal or unequal. Capsule substipitate, ellipsoid to obovoid, retinacula present, septae with attached retinacula remaining attached to inner wall of mature capsule. Seeds 4 (or fewer by abortion), homomorphic, lenticular. ($x = 13$).

This genus of 15 species is restricted to, but occurs nearly throughout, the dry regions of Mexico (Daniel 1983b, 1988b).

1. Leaves opposite (or subopposite); inflorescence of terminal spikes to 15 cm long. . *H. virgata*
1. Leaves quaternate; inflorescence of axillary spikes to 3.7 cm long. . . . . *H. pallida*

Holographis pallida Leonard & Gentry in H.S. Gentry, Brittonia 6:324. 1948. TYPE: MEXICO. Sinaloa: Cerro Llano Redondo, W of Caymanero, 25 Apr 1944, *H. Gentry 7022* (holotype: MICH!; isotypes: ARIZ!, F!, GH!, NY!, US!).

Phenology. February–April; fruiting: March–April.

Distribution and habitats. Northwestern Mexico (Sinaloa, Sonora); Sonoran plants occur on slopes and along watercourses in thornscrub and tropical deciduous forests at elevations from 50 to 600 m.

Illustrations. Figure 15; *Brittonia* 6:325. 1948.

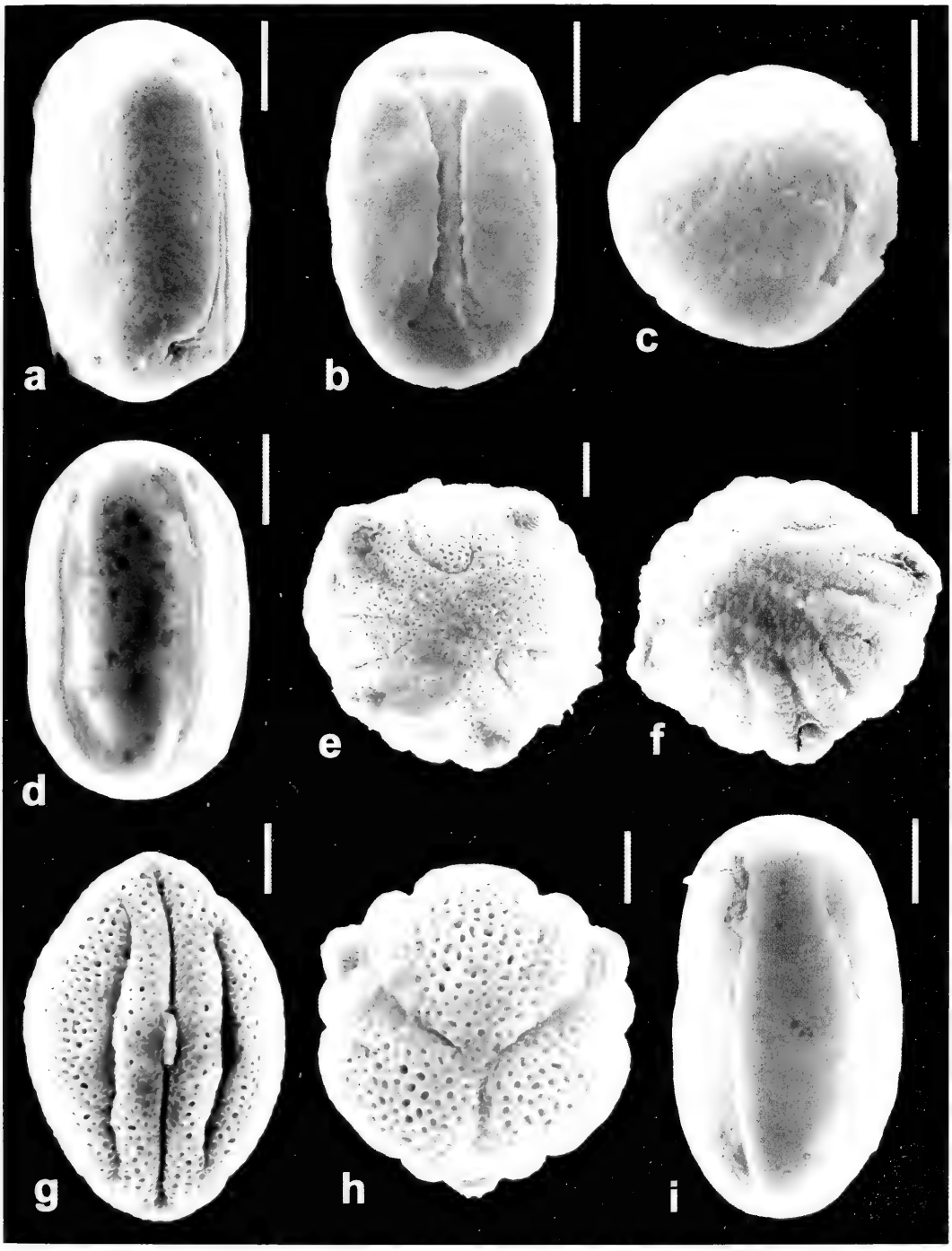


FIGURE 18. Pollen of Sonoran Acanthaceae. a. *Holographis pallida* (*Daniel 3382*), interapertural view. b. *H. pallida* (*Daniel 3382*), apertural view. c. *H. pallida* (*Daniel 3382*), polar view. d. *H. virgata* (*Breedlove 60981*), interaperatural view. e. *Odontonema cuspidatum* (*Jenkins & Yetman 91-115*), polar view. f. *O. cuspidatum* (*Breedlove & McClintock 23784*), polar view. g. *Pseuderanthemum praecox* (*McVaugh 26541*), apertural view. h. *P. praecox* (*Daniel 2131*), polar view. i. *Stenandrium pilosulum* (*Moran 21965*), interapertural view. Scales = 10 μm.

Local name. "Ramito chino" (*Gentry 1350*).

Daniel (1983b) provided a description of this species, which is endemic to northwestern Mexico. Its corollas are white to greenish white with light pink stripes on the lobes of the lower lip. *Holographis pallida* reaches the northern extent of its distribution in east-central Sonora (Fig. 19).

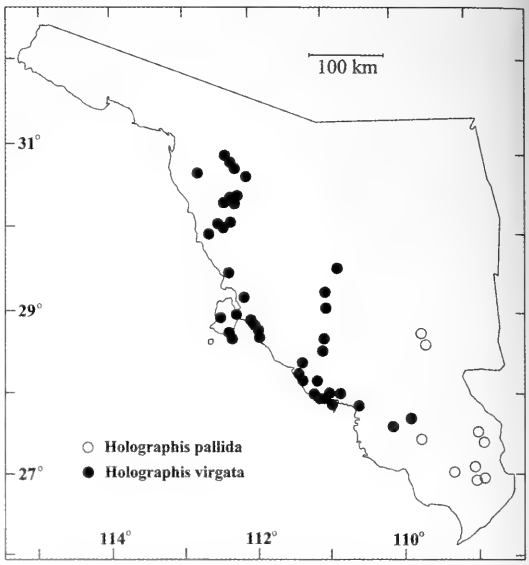


FIGURE 19. Sonoran distributions of *Holographis pallida* and *H. virgata*.

SONORAN COLLECTIONS: Arroyo Cuchujaqui, 7.4 mi SE of Alamos on road to Guiricoba, *T. Daniel 3382* (ASU, CAS), *3996* (CAS); Mpio. Soyopa, crossing of Río Yaqui with Hwy. 16, 8.5 km W of jct. to Onavas, ca. 28°34′N, 109°33′W, *T. Daniel et al. 8510* (ASU, BR, CAS, K, MEXU, MICH, MO, US); San Bernardo, *H. Gentry 1350* (A, ARIZ, F, MEXU, MO, UC, WIS), *3615* (ARIZ, F); Sierra Bojihuacame SE of Cd. Obregón, *H. Gentry 14492* (ARIZ, US); NE side of Río Yaqui bridge on Mex. 16, just S of Tonichi, ca. 28°34′N, 109°33′W, *A. Reina G. et al. 97-947* (CAS); Río Cuchujaqui, 8 mi SE of Alamos, ca. 26°56′N, 108°53′W, *A. Sanders 3685* (CAS); Mpio. Alamos, Cerro La Luna, ca. 14 km NW of Alamos, ca. 27°07′N, 109°02′W, *A. Sanders et al. 13257* (ARIZ, CAS, TEX, US); Río Cuchujaqui at Rancho El Conejo, 12.4 km S of Alamos, 26°55′N, 108°55′W, *T. Van Devender 92-562* (ARIZ); Cerro Prieto, ca. 9 mi E of Navojoa on Alamos Road, 27°05′N, 109°17′W, *T. Van Devender et al. 92-166* (ARIZ, CAS); below Guajaray on Arroyo Guajaray, 6.5 km WNW of jct. with Río Mayo, 27°36′N, 108°56′W, *T. Van Devender et al. 93-465* (ARIZ, CAS, TEX); between Rancho La Junta on Río Mayo and Guajaray on Arroyo Guajaray, 27°35–36′N, 108°52–56′W, *T. Van Devender et al. 93-504* (ARIZ, CAS); Mpio. Soyopa, Mina Soyopita, 1 km S of Soyopa, W side of Río Yaqui, 28°46′N, 109°38′W, *T. Van Devender et al. 99-911* (CAS).

Holographis virgata (Harv. ex Benth. & Hook.f.) T.F. Daniel, J. Arnold Arbor. 64:139. 1983. *Berginia virgata* Harv. ex Benth. & Hook.f., Gen. Pl. 2:1097. 1876. TYPE: MEXICO. State unknown: "California incola," *T. Coulter 603* (holotype: K!; isotypes: BM!, GH!, K!).

Pringleophytum lanceolatum A. Gray, Proc. Amer. Acad. Arts 20:293. 1885. TYPE: MEXICO. Sonora: 50 mi below Altar and 30 mi from Gulf of California, 13 Mar 1884, *C. Pringle s.n.* (holotype: GH!; isotypes: A!, F!, G!, MA!, NY!, P!, US!, WIS!).

Phenology. Flowering: December–May; fruiting: March–May.

Distribution and habitats. Northwestern Mexico (Baja California, Baja California Sur, Sonora); Sonoran plants occur on rocky slopes and along watercourses in Sonoran desertscrub (Central Gulf Coast, Lower Colorado River Valley, Plains of Sonora) and thornscrub at elevations from 15 to 442 m.

Illustrations. Figure 15; *Proceedings of the California Academy of Sciences* 49:348. 1997.

Local name. "?áayaam" (Seri, *Felger et al. 17831*).

Daniel (1983b, 1997) provided descriptions of this species and its infraspecific taxa. Corollas of *Holographis virgata* have a white tube, light pink to whitish upper lip, and a dark pink lower lip with white veins (and a white area near the mouth) on the lobes of the lower lip. *Holographis virgata* subsp. *virgata* is the only infraspecific taxon present in Sonora. Both the species and the nominate subspecies attain their northern and eastern distributional limits in Sonora (Fig. 19).

Sonoran collections: 12 mi NW of Hermosillo, *L. Abrams 13305* (DS, F); canyon back of Palma, 40 mi S of Hermosillo, *L. Abrams 13348* (DS); Isla Tiburón, *J. Alcocer & C. Sosa R. 6* (ENCB); ca. 31 mi E of Punta Cirio between Puerto Libertad and Caborca, *J. Bowers & S. McLaughlin 1613* (ARIZ); S side of Algodones Bay, 2 km W of Cerro Tetas de Cabra, 27.9°N, 111.0°W, *T. Burgess et al. 6363* (ARIZ, ENCB, MEXU); ca. 3.5 km E of El Caracol, 30°02′N, 112°26′W, *T. Burgess et al. 6439* (ARIZ); El Himalaya (Peña Blanca), entre San Carlos y Tastiota, 28°11′N, 111°20′W, *A. Búrquez et al. 91-312* (MEXU); 10 mi NW of Hermosillo, *C. Carter s.n.* (MICH); "Microondas mountain" overlooking Guaymas, along road which is 1.8 mi from Mex. Hwy. 15 on paved road to airport, N of Guaymas, *T. Daniel 1958* (ASU); Nacapuli Canyon, 6.3 mi W of Hwy. 15 on road to San Carlos then 4.4 mi N, *T. Daniel 1969* (ASU), 1972 (ASU, CAS); near Guaymas, *E. Dawson 1075* (F, MICH); San Miguel de Horcasitas, *G. Eisen s.n.* (PH, US); N end of Bahía San Carlos, *R. Felger 2671* (ARIZ); 2.7 mi E of Tajitos on Mex. 2 (between Sonoyta and Caborca), *R. Felger 7419* (ARIZ); 10.2 mi S of La Pintada on Hwy. 15 (between Hermosillo and Guaymas), *R. Felger 8381* (CAS); Isla Turners (= Datil), island off S shore of Isla Tiburón, 28°43′N, 112°17′W, *R. Felger 9082* (ARIZ, CAS); NE end of Bahía San Carlos, *R. Felger 9617* (CAS); Isla Turners (=Datil), 28°43′N, 112°17.5′W, *R. Felger & J. Cooper 15320* (ARIZ); Sierra del Viejo (SW of Caborca), *R. Felger & H. Gentry 7912* (ARIZ); Bahía Colorado, ca. 28°18′N, 111°28′W, *R. Felger & E. Hamilton 15683* (CAS); ca. 0.5 mi SE of Cañón Nacapules, ca. 6 km NE of Bahía San Carlos, ca. 28°10′N, 111°03.5′W, *R. Felger & R. Thomas 11957* (ARIZ); ca. 0.8 mi N of Bahía San Carlos toward Bahía Algadones, *R. Felger & R. Thomas 12027* (CAS); Cerro San Nicolas, W of S end of Kino estuary, *R. Felger et al. 9555* (ARIZ); Ensenada Grande (= Bahía San Pedro), *R. Felger et al. 11616* (CAS); Isla Tiburón, ca. 13 mi S of Tecomate, ca. 28°57′N, 112°27′W, *R. Felger et al. 12384* (ARIZ), *12397* (ARIZ); Isla Tiburón, vicinity of Palo Fierro, Punta Tortuga, *R. Felger et al. 12555* (ARIZ, ENCB); Tiburón Island, Ensenada de la Perra, ca. 28°47′N, 112°16′W, *R. Felger et al. 17730* (ARIZ); vicinity of Rancho Arivaipa, ca. 8 mi ENE of Pozo Coyote, ca. 29°37′N, 112°17′W, *R. Felger et al. 17831* (ARIZ, CAS, MEXU); Cañón Nacapules, ca. 6 km N of Bahía San Carlos, ca. 28°10′N, 111°03′W, *R. Felger et al. 85-565* (ARIZ, CAS, MEXU); Picu Mts., Altar Distr., *H. Gentry 4479* (ARIZ, MICH, MO); Sierra Cajón del Diable, *H. Gentry 11622* (ARIZ, LL, MEXU, MICH); Bahía Algadones, San Carlos, Guaymas, *D. Goldberg 77-71* (ARIZ); 22.2 mi N of Bahía Kino Nuevo, *J. Hastings & R. Turner 64-40* (ARIZ, DS, SD); 0.9 mi E of Pitiquito, *J. Hastings & R. Turner 64-58* (ARIZ, DS, SD); 8 mi ESE of Vicam along Hwy. 15, 27.6°N, 110.2°W, *J. Hastings & R. Turner 69-64* (ARIZ); W of Obregón, *P. Jenkins 89-317* (ARIZ, CAS); Guaymas, *I. Johnston 3114* (CAS, GH, US); Hermosillo, *M. Jones 22531* (MEXU, MO); 8 mi NW of Caborca toward Tajitos, *D. Keck 4059* (C, CAS, DS, F, MO, NY); Mpio. Pitiquito, 54 km S of Pitiquito toward Puerto de la Libertad, ca. 11 km SW of Bimuri, 30°17′N, 112°07′W, *G. Levin 2172* (CAS, MEXU); near Pozo Cerna, *Long 62* (US); Isla Tiburón, *E. Lott & T. Atkinson 2518* (CAS, MEXU, TEX); New Kino, Bahía Kino, *W. Mahler & J. Thieret 6070* (SUM); N de Guaymas, *F. Miranda 8943* (MEXU), *8944* (MEXU); Tiburón Island, 28°46′N, 112°18′W, *R. Moran 4065* (DS, SD, UC); Guaymas, *E. Palmer 307* (GH); Las Guásimas, *R. Perrill 5353* (ARIZ); Mpio. Empalme, Rancho las Trincheras, ca. 6 km NW of Empalme, 28°01′N, 110°50′W, *A. Reina G. & T. Van Devender 2001-182A* (ARIZ, CAS); Guaymas area, near Rancho El Valiente, at jct. Hwy. 15 with bypass to Cd. Obregón, 3.8 mi N of turnoff to San Carlos Bay, ca. 28°02′N, 110°56′W, *A. Sanders et al. 8767* (MO); near Rancho Verruga, Distr. Altar, *F. Shreve 5823* (ARIZ, US); 5 mi NW of Caborca, *F. Shreve 7531* (ARIZ); 15 mi NW of Caborca, *F. Shreve 7553* (ARIZ, F, MICH, MO, US); ca. 20 mi NE of Obregón, *W. Spaulding 75-3-12* (ARIZ); Sierra Libre, 28°34.5′N, 110°58′W, *G. Starr 752* (ARIZ); 0.2 mi W of Rancho San Alfroso, 28.2°N, 111.2°W, *R. Turner & L. Duek 79-37* (ARIZ); 5.8 mi NW of Kino Bay on road to Punta Chueca, *R. Van Devender & T. Van Devender 83-96* (ARIZ, MEXU); Puerto Los Mochos, Rancho Los Mochos, ca. 20 mi NNE of Desemboque de San Ignacio, *T. Van Devender & M. Kearns s.n.* (ARIZ); Mpio. Hermosillo, Playa Esthela, just N of Bahía de Kino, 28°52′N, 112°01′W, *T. Van Devender & A. Reina G. 2000-932* (CAS, MEXU); Nacopuli Canyon, ca. 4 mi N of San Carlos Bay, *T. Van Devender et al. 84-239* (ARIZ); 8.6 mi NW of Caborca, *I. Wiggins 8268* (ARIZ, DS, TEX); Sierra Seri, ca. 29°17′N, 112°08′W, *R. Wilkinson s.n.* (ARIZ); Sierra del Viejo, 0.5 mi NE of Mina de la Santa Cruz, 30°23′N, 112°22′W, *G. Yatskievych & P. Fischer 82-04* (ARIZ).

Justicia L.

Justicia L., Sp. Pl. 1:15. 1753, nom. cons. prop. LECTOTYPE (Hitchcock and Green, International Botanical Congress, Cambridge (England), 1930: Nomenclature Proposals by British Botanists. 116. 1929): *Justicia hyssopifolia* L.

Dianthera L., Sp. Pl. 1:27. 1753. TYPE: *Dianthera americana* L. (≡ *Justicia americana* (L.) Vahl).

Adhatoda Mill., Gard. Dict. Abr. ed. 4, 1:[*Adhatoda* in alph. seq.]. 1754. TYPE: *Adhatoda* "*zeylanensium*" Mill. fide Graham (1988); *Adhatoda vasica* Nees = lectotype fide Index Nominum Genericorum (as of information dated 9 Feb 1996 at http://rathbun.si.edu/botany/ing/); both names pertain to *Justicia adhatoda* L.

Beloperone Nees in N. Wallich, Pl. Asiat. Rar. 3:76. 1832. LECTOTYPE (Bremekamp, Index Nom. Gen. Card 00123. 1955): *Beloperone amherstiae* Nees (≡ *Justicia brasiliana* Roth).

Sericographis Nees in Martius, Fl. Bras. 9:107. 1847. LECTOTYPE (Bremekamp, Index Nom. Gen. Card 02841. 1957): *Sericographis rigida* Nees (≡ *Justicia sericographis* V.A.W. Graham).

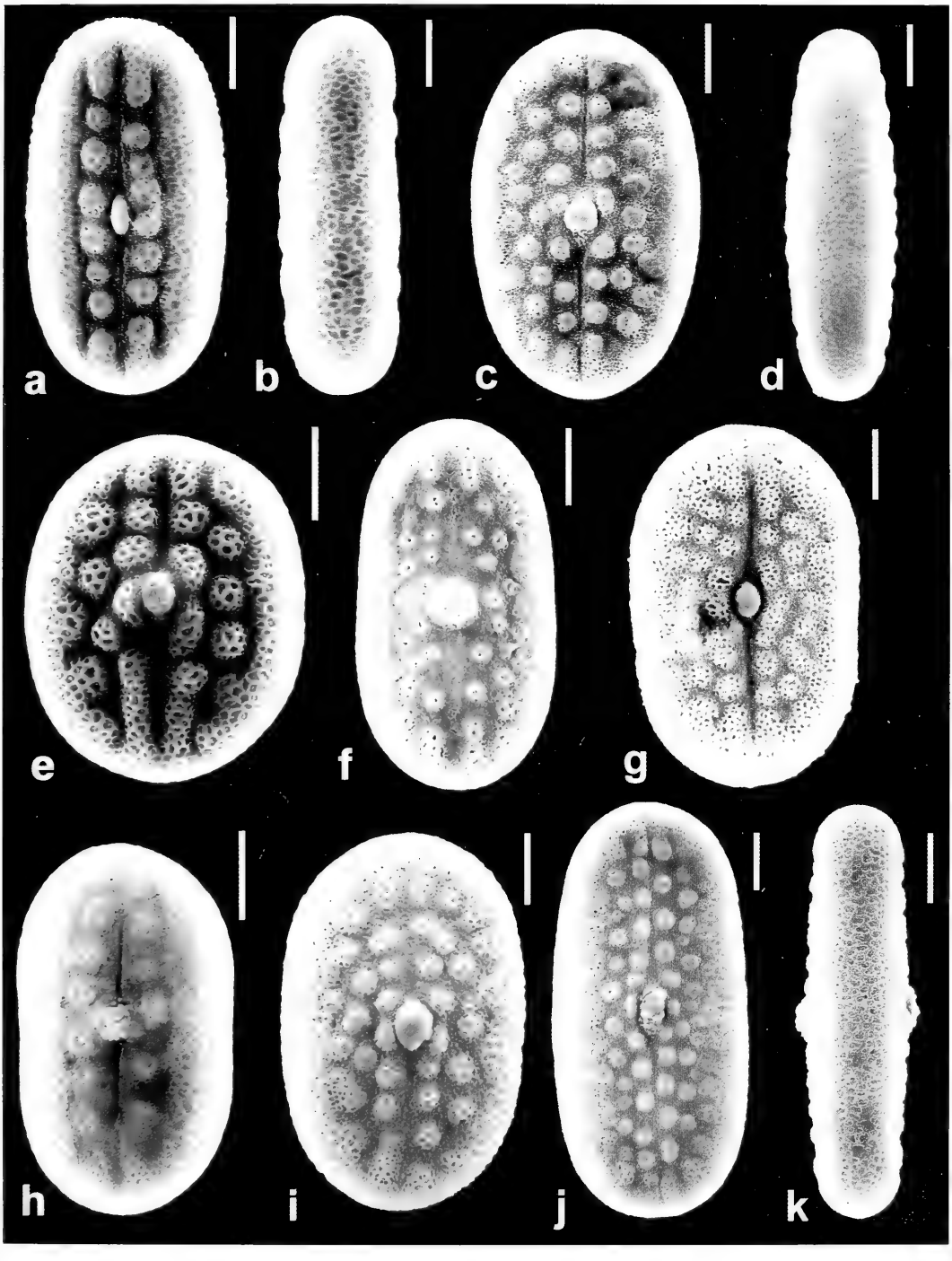
Sarotheca Nees in Martius, Fl. Bras. 9:113. 1847. LECTOTYPE (Bremekamp, Index Nom. Gen. Card 01996. 1956): *Sarotheca elegans* Nees (≡ *Justicia sarotheca* V.A.W. Graham).

Jacobinia Nees ex Moric., Pl. Nouv. Amér. 156. 1847, nom. cons. TYPE: *Jacobinia lepida* Nees (≡ *Justicia lepida* (Nees) Wassh.).

Siphonoglossa Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:159. 1855. TYPE: *Siphonoglossa ramosa* Oerst. (≡ *Justicia ramosa* (Oerst.) V.A.W. Graham).

Decumbent to erect perennial herbs, shrubs, or small trees with cystoliths. Leaves opposite. Inflorescence of dichasia in leaf axils (or in axil of 2 partially fused bracts forming a cupulate involucre) or of axillary or terminal dichasiate spikes, racemes, or thyrses, inflorescences sometimes branched and becoming panicles; dichasia alternate or opposite, 1 (–3)-flowered, sessile or pedunculate, subtended by a leaf or a bract. Flowers homostylous, sessile or pedicellate, subtended by 2 homomorphic bracteoles. Calyx deeply 4–5-lobed, lobes equal or unequal in size, posterior lobe sometimes greatly reduced in flowers with 5 calyx lobes. Corolla greenish, white, yellow, orange, pink, red, or purple, usually with white or colored markings (often restricted to lower lip), tube cylindric to expanded distally, usually lacking a distinct throat, limb strongly zygomorphic, 2-labiate, upper lip internally rugulate (i.e., with a stylar furrow), comprising 2 fused lobes, entire to 2-lobed, lower lip 3-lobed, corolla lobes imbricate in bud. Stamens 2, exserted from mouth of corolla, anthers 2-thecous (1 theca rarely sterile), thecae equal or unequal in length, parallel to perpendicular, equally inserted on filament, unequally inserted (but overlapping for some portion of their length), or superposed (i.e., not overlapping), 1 or both with a basal appendage or appendages absent, dehiscing toward lower lip (i.e., flower nototribal); pollen (Figs. 20–21) subprolate to perprolate, 2–4-aperturate (varying from porate to colporate with distinctness of colpi sometimes questionable), apertures flanked on each side by 1-several rows of ± circular insulae and/or peninsulae or by both a solid band of exine and a pseudocolpus, exine variously ornamented but usually reticulate; staminodes 0 (although pubescent thickenings near attachment of filaments rarely

FIGURE 20 (right). Pollen of Sonoran *Justicia*. a. *J. californica* (*Daniel 1542*), apertural view. b. *J. californica* (*Daniel 1542*), interapertural view. c. *J. candicans* (*Daniel 8355*), apertural view. d. *J. candicans* (*Daniel 8355*), interapertural view. e. *J. hilsenbeckii* (*Lott & Guadalupe A. 2656*), apertural view. f. *J. caudata* (*Breedlove & Daniel 70945*), apertural view. g. *J. phlebodes* (*Van Devender et al. 93-483*), apertural view. h. *J. salviiflora* (*Raven & Breedlove 20133*), apertural view. i. *J. sonorae* (*Van Devender & Reina G. 98-434*), apertural view. j. *J. spicigera* (*Avila B. 28*), apertural view. k. *J. spicigera* (*Avila B. 28*), interapertural view. Scales = 10 μm.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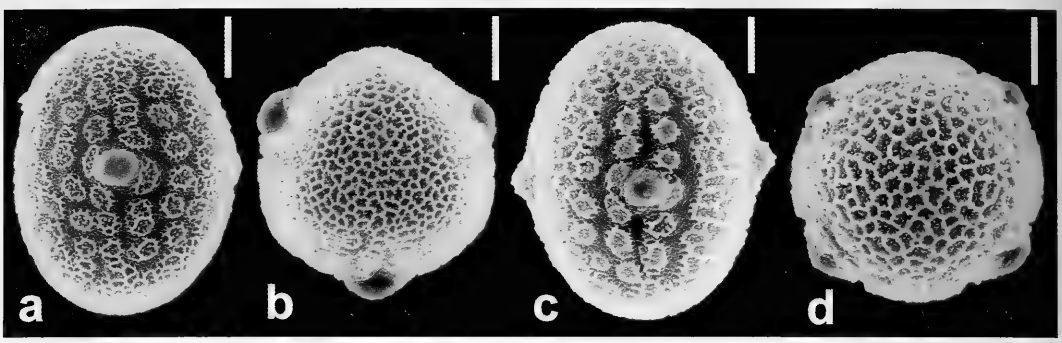


FIGURE 21. Pollen of Sonoran *Justicia*. a. *J. longii* (*Butterwick & Hillyard 7384*), apertural view. b. *J. longii* (*Butterwick & Hillyard 7384*), polar view. c. *J. masiaca* (*White 3590*), apertural view. d. *J. masiaca* (*White 3590*), polar view. Scales = 10 μm.

present). Style exserted from mouth of corolla, stigma lobes indistinct to distinct, when distinct equal to unequal in length (1 lobe sometimes vestigial). Capsule stipitate, retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule. Seeds 2-4, homomorphic, lenticular to globose. (x = 11, 14).

Justicia is the largest genus of Acanthaceae with estimates of up to 600 species worldwide. It is also the largest genus of the family in Mexico (ca. 100 species) and in Sonora (10 species). Morphological diversity in the genus is extensive and the above generic description is derived from North and Central American species only. The generic synonymy given above only includes genera in which species from our region have been previously treated. Daniel (1995a) provided a more complete listing of generic synonyms in which American species have been treated. Graham (1988) presented a comprehensive generic account of *Justicia* that includes generic synonyms on a worldwide basis.

1. Calyx 4-lobed with lobes homomorphic or 5-lobed with lobes heteromorphic (posterior lobe greatly reduced in size with respect to other 4 lobes); capsule pubescent with glandular and eglandular trichomes.
    2. Corolla cream or greenish with pink and maroon markings, tube 6–10.5 mm long; both thecae dorsally pubescent; capsule 14–20 mm long; seeds covered with barbed bristles. ..... *J. salviiflora*
    2. Corolla pink to pale purplish, often with white markings on lower lip, tube 11–23.5 mm long; thecae glabrous (or sometimes with the upper theca pubescent); capsule 7–13.5 mm long; seeds tuberculate (lacking bristles).
        3. Corolla tube gradually expanded from near base to apex, 1.8–2.7 mm in diameter near midpoint, lower lip 8–17 mm long; thecae subequally inserted; capsule 10–13.5 mm long. ..... J. *sonorae*
        3. Corolla tube cylindric (expanded only near mouth), 0.6–1.2 mm in diameter near midpoint, lower lip 4–7 mm long; thecae unequally inserted or superposed; capsule 7–10 mm long.
            4. Bracteoles 2–4.5 mm long, 0.2–0.4 mm wide; calyx 3–5 mm long, lobes subulate to lance-subulate; thecae unequally inserted (overlapping by 0.6–0.8 mm), lacking basal appendages; seeds 2.2–2.5 mm long..... *J. hilsenbeckii*
            4. Bracteoles 4.8–6.5 mm long, 0.5–0.7 mm wide; calyx (5-) 6.5–9 mm long, lobes linear; thecae superposed (separated by a gap 0.4–0.7 mm long), lower theca with a basal

appendage; seeds 1.5–1.7 mm long. . . . . *J. phlebodes*

1. Calyx 5-lobed, lobes homomorphic; capsule glabrous, pubescent with eglandular trichomes only, or pubescent with both eglandular and glandular trichomes.
   5. Bracts of axillary spikes heteromorphic, sterile bracts greatly reduced in size; calyx white-hyaline along margin; corolla externally pubescent with eglandular and conspicuous glandular trichomes, tube 5–8 mm in diameter near midpoint; thecae green; seeds smooth and puberulent. . . . . *J. caudata*
   5. Bracts (if present) homomorphic, sterile bracts (if present) similar to fertile bracts; calyx not white-hyaline along margin; corolla externally pubescent with eglandular trichomes only (infrequently with a few glandular trichomes in J. californica) or glabrous distally and very inconspicuously glandular proximally (J. spicigera), tube 1–4 mm in diameter near midpoint; thecae not green (often reddish); seeds smooth to tuberculate or covered with subconic papillae, lacking trichomes.
      6. Perennial herbs to 5 dm tall; corolla tube cylindric (expanded only near mouth), 1–1.5 mm in diameter near midpoint; calyx lobes widest above the base (i.e., narrowed proximally); pollen 3–4-aperturate; seeds bubbly tuberculate.
         7. Corolla purple (limb) and white (tube), tube 12.5–33 mm long; style 11–33 mm long; pollen 4-aperturate. . . . . *J. masiaca*
         7. Corolla entirely white, tube 23–43 mm long; style (23-)32–40 mm long; pollen 3-aperturate. . . . . *J. longii*
      6. Shrubs to 3 (or more) m tall; corolla tube gradually expanded from near base to apex, 1.7–4 mm in diameter near midpoint; calyx lobes widest at base; pollen 2-aperturate; seeds smooth to lumpy or covered with subconic papillae.
         8. Inflorescence of axillary panicles of dichasiate spikes; bracteoles abaxially glabrous or inconspicuously glandular-punctate; corolla orange, fusiform in bud, externally glabrous distally and inconspicuously pubescent with a few subsessile glandular trichomes to 0.1 mm long proximally, tube 19–32 mm long, lower lip recoiled; seeds covered with subconic papillae; introduced plants (cultivated or escaping). . . . . *J. spicigera*
         8. Inflorescence of dichasia in leaf axils, condensed dichasiate spikes (often appearing as clusters) in leaf axils, or (axillary or) terminal dichasiate thyrses; bracteoles abaxially pubescent with eglandular and sometimes stipitate glandular trichomes as well; corolla red (sometimes with white markings), linear-ellipsoid in bud, externally pubescent with eglandular (and sometimes also with stipitate glandular) trichomes to 0.5 mm long, tube 11–20 m long, lower lip not recoiled; seeds smooth to lumpy (i.e., covered with irregular, low, rounded bumps); native plants (rarely cultivated).
            9. Young stems ± pallid resulting from a dense and even covering of very short trichomes, the epidermis not (or but barely) visible; inflorescence of (axillary or) terminal dichasiate thyrses; dichasia pedunculate, peduncles 1–14 mm long; corolla entirely red, lobes of lower lip 1–5.5 mm long; thecae dorsally pubescent, lower (and sometimes upper) theca with a prominent basal appendage to 0.6 mm long; capsule pubescent; seeds subglobose to ± compressed, not red. . . . . *J. californica*
            9. Young stems glabrous or pubescent but not pallid as described above, the epidermis usually clearly visible; inflorescence of solitary dichasia in leaf axils or condensed dichasiate spikes (appearing as clusters) in leaf axils; dichasia sessile; corolla red with white markings on lower lip, lobes of lower lip 4.5–11.5 mm long; thecae dorsally glabrous, lacking basal appendages (or rarely the lower theca with an incon-

spicuous basal appendage to 0.1 mm long); capsule glabrous; seeds sublenticular, usually somewhat reddish. ..... *J. candicans*

Justicia californica (Benth.) D.N. Gibson, Fieldiana, Bot. 34:67. 1972. *Beloperone californica* Benth., Bot. Voy. *Sulphur*, 38. 1844. *Jacobinia californica* Nees in A. de Candolle, Prodr. 11:729. 1847. *Sericographis californica* (Benth.) A. Gray in Torrey in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):125. 1859. TYPE: MEXICO. Baja California Sur: Cape St. Lucas, 1841, *R. Hinds s.n.* (holotype: K!).

Phenology. Flowering: throughout the year, but with a peak in March(–April) and only sporadically in other months (Fig. 1); fruiting: throughout the year.

Distribution and habitats. Southwestern United States (Arizona, California), northwestern Mexico (Baja California, Baja California Sur, Sinaloa, Sonora); Sonoran plants occur on coastal dunes, along watercourses, and on rocky slopes in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Lower Colorado River Valley, Plains of Sonora), thornscrub, and grasslands at elevations from sea level to 1046 m.

Illustrations. Figure 6; *Flora of Baja California*, 188. 1980; *Trees and Shrubs of the Southwestern Deserts*, 3rd. ed., 218. 1981; *Desert Plants* 5:169. 1984; *The Jepson Manual, Higher Plants of California*, 127. 1993; *Flora of the Gran Desierto and Río Colorado of Northwestern Mexico*, 65. 2000.

Local names. "Chuparosa" or "chuparrosa" (fide Felger 2000 and Felger and Moser 1985; *Búrquez 95-123, Búrquez et al. 91-280, Rea 1200, Nabhan et al. 249*, etc.); "hummingbird bush" (fide Felger 2000); "koo-me-me" (Guarijío, *Gentry 1291*); "noj-oopis" (Seri, fide Felger and Moser 1985); "semaluca" (Mayo, *Van Devender et al. 94-386*); "sewalulukut" (Yaqui, fide Felger 1999); "vipsumar hiosik" (Pima Bajo, *Rea 1200*); "wipisimal" (fide Felger 2000); "wipisomal" (Papago, *Bowers & Nabhan 172*, *Nabhan et al. 249*).

Uses. Source of food (floral nectar) for pre-Columbian cultures (Hodgson 2001).

Daniel (1997) provided a description of this species. Its distribution is nearly restricted to the Sonoran Desert of the southwestern United States and northwestern Mexico, where it is usually found in or along watercourses. In Sonora, it is widespread throughout western, central, and southern portions of the state (Fig. 22). Felger (2000) noted that in northwesternmost Sonora, the flowers attract Costa's, Rufous, and Allen's hummingbirds, as well as honeybees and butterflies. He also noted that carpenter bees (*Xylocopa*) and sometimes hummingbirds slit the floral tube and consume nectar. Other collectors have noted hummingbird visitation to flowers of *Justicia californica* from other portions of its range in Sonora (e.g., *Parfitt & Reeves 2398* notes visitation by Anna's and either Rufous or Allen's hummingbirds in west-central Sonora). Turner et al. (1995) noted additional ecological aspects of the species.

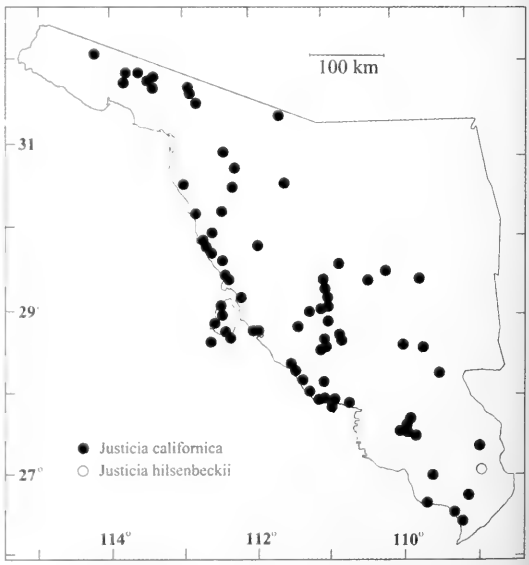


FIGURE 22. Sonoran distributions of *Justicia californica* and *J. hilsenbeckii*.

Sonoran collections: Sierra Bacha, ca. 17 km SE of Puerto Libertad, ca. 29°47′N, 112°33.5′W, *E. Abbey & R. Felger 20245* (ARIZ); 40 mi S of Hermosillo, *L. Abrams 13350* (DS); Guaymas, *R. Barr & W. Brewer 63-651* (ARIZ, MEXU); Kino Bay, *R. Barr & W. Brewer 63-663* (ARIZ, MEXU); Bahía San Carlos, Perinola Palms, ca. 7 mi N of Bahía San Carlos, *F. Boutin & F. Brandt 2827* (MEXU); Quitovac, between Sonoyta and Caborca, *J. Bowers & G. Nabhan 172* (ARIZ); Guaymas, *T. Brandegee s.n.* (UC); Mpio. San Luis Colorado, 11.4 mi S of Sonoita on Mex. 2, *D. Breedlove 1457* (DS, DUKE); Mpio. Hermosillo, 7 mi W of Hwy. 15 toward Bahía Kino, *D. Breedlove 15942* (DS, ENCB); Sierra del Viejo, 7 km N and 3 km E of El Plomito, 30°19′N, 112°20′W, *T. Burgess 5772* (ARIZ); Cañada Tetabejo, Sierra Libre, S de Hermosillo, 28°33′N, 110°58′W, *A. Búrquez 95-123* (MEXU); 2.5 km S de Hermosillo, 29°01′N, 110°57′W, *A. Búrquez & M. Quijada 90-179* (MEXU), *91-90* (MEXU), *A. Búrquez & M. Quintana 94-204* (MEXU); Cañón las Cocinas, entre San Carlos y Tastiota, 28°16′N, 111°23′W, *A. Búrquez et al. 91-280* (MEXU); 59 km SE de Caborca, 30°37′N, 111°36′W, *A. Campos V. et al. 4427* (CAS, MEXU); S Sonoyta, *O. Clark 11369* (UNM); N Guaymas, *O. Clark 14957* (UNM); Mpio. Hermosillo, S of Moro Colorado, 5 mi SSE of Estero Tastiota, *J. Copp 70-10* (CAS); Gran Desierto, SE side of Sierra del Rosario, ca. 32°05′N, 114°10.5′W, *H. Coss et al. 20389* (ARIZ, ENCB); Torres, *F. Coville 1651* (NY, US); near KM 74, Calle 4 Sur (diagonal road from Mex. 15 S of Hermosillo to Mex. 16 W of Hermosillo), *G. Cummins s.n.* (ARIZ); between Hermosillo and Kino Bay, 2.5 mi E jct. Son. 16 (Calle 4 Sur) to Guaymas, *T. Daniel 942* (CAS); "Microondas mountain" overlooking Guaymas, along road which is 1.8 mi from Mex. Hwy. 15 on paved road to airport, N of Guaymas, *T. Daniel 1956* (ASU, CAS); Nacapuli Canyon, 6.3 mi W of Hwy. 15 on road to San Carlos then 4.4 mi N, *T. Daniel 1992* (ASU); 1.6 mi NE of Masiaca toward Alamos, 7.1 mi NE Hwy. 15, *T. Daniel 2547* (CAS); along road between Hwy. 16 E of Tonichi and Movas, 15.8 mi S of Onavas, *T. Daniel 3354* (CAS); W base of Sierra Bojihuacame E of Cd. Obregón, 1.2–2.2 mi SE of Bachoco, *T. Daniel 3368* (CAS); ca. 2 mi E of San Carlos (NW of Guaymas), *T. Daniel 3976* (CAS); Bahía Kino, N of village, *F. Drouet & D. Richards 3518* (DS, F, US); NW edge of Guaymas, *F. Drouet & D. Richards 4033* (F); along Hwy. 15 ca. 2 mi N of jct. to Becachibampo Bay, *D. Dreyer 218* (CAS); Sierra de Calera E of Villa de Seris, *F. Drouet et al. 3398* (F); San Carlos Bay, ca. 7 mi W of Hwy. 15, *E. Engle 29* (MEXU); Pinacaté, derrame de lava en Campo Rojo, 31°45′N, 113°27′W, *M. Equihua s.n.* (ARIZ, MEXU); ca. 2 mi E of Esperanza (several mi N of Cd. Obregón, *R. Felger 360* (ARIZ); 1.8 mi NW of town of Bahía Kino, *R. Felger 2513* (ARIZ, MEXU); A. Rodríguez Dam, E side of Hermosillo, Río Sonora, *R. Felger 2785* (ARIZ, MEXU, TEX); Sau Sal landing field, S end of Tiburón Island, *R. Felger 6436* (ARIZ); NW part of Isla Tiburón, vicinity of Tecomate, Arroyo Agua Dulce, *R. Felger 6828* (ARIZ); Isla San Esteban, *R. Felger 7057* (CAS), *R. Felger et al. 17597* (CAS, MEXU); 2.2 mi W of Tajitos (NW of Caborca), *R. Felger 7450* (ARIZ); Isla Cholludo, between Isla Tiburón and I. Turners, *R. Felger 9162* (ARIZ); Hourglass Canyon, ca. 2 mi NE of Huarache Tank, W side of Pinacate region, *R. Felger 19136* (ARIZ, ENCB, GH); SW part of Pinacate region, ca. 1 km S of Tule Tank, *R. Felger 19228-F* (ARIZ); 1.3 mi N of village of Bahía Kino and ca. 1 km inland from shore, *R. Felger & J. Cooper 15251* (ARIZ); Isla San Esteban, N side of island, *R. Felger & J. Cooper 15408* (MEXU); Bahía Colorado, E base of Morro Colorado, ca. 28°18.5′N, 111°28′W, *R. Felger & E. Hamilton 15667* (ARIZ); ca. 5 mi N of El Desemboque San Ignacio, *R. Felger & M. Moser 5240* (ARIZ); Rancho San Jorge, ca. 20 mi W of Hermosillo, *R. Felger & A. Russell 6892* (ARIZ, MEXU); 1 mi N of Bahía San Carlos on road to Algadones, *R. Felger & A. Russell 9590* (ARIZ, MEXU); Isla Tiburón, ca. 13 mi S of Tecomate, ca. 28°57′N, 112°27′W, *R. Felger & A. Russell 12356* (ARIZ, ENCB, MEXU, UC); Isla Cholludo, between Isla Tiburón and I. Turners, *R. Felger & O. Soule 13414* (ARIZ); Cañón Nacapules, ca. 4 km N of Bahía San Carlos, *R. Felger & R. Thomas 11992* (ARIZ, MEXU); 11.8 mi S of Sonoyta, *R. Felger et al. 9824* (ARIZ); Ensenada Grande (= Bahía San Pedro, N of Guaymas), *R. Felger et al. 11600* (ARIZ); Isla Tiburón, vicinity of Tecomate, NW part of island, *R. Felger et al. 12527* (ARIZ); Isla Alcatraz, Bahía Kino, *R. Felger et al. 12723* (ARIZ); Isla San Esteban, E-central side of island, *R. Felger et al. 12763* (ARIZ); N side of Cerro Tepopa, SW of El Desemboque San Ignacio, ca. 29°22′N, 112°24′W, *R. Felger et al. 14141* (ARIZ, CAS); Pinacate Region, Tinaja Chivos, ca. 31°45′N, 113°36.5′W, *R. Felger et al. 18609* (ARIZ); Pinacate Region, E side of Sierra Blanca, ca. 31°34′N, 113°26′W, *R. Felger et al. 20210* (ARIZ); Sierra del Rosario, ca. 32°06′N, 114°11.5′W, *R. Felger et al. 20738* (ARIZ, ENCB); Sierra del Rosario, ca. 32°06', 114°11′W, *R. Felger et al. 75-15* (ARIZ, ENCB, MEXU); Cañón Nacapules, ca. 6 km N of Bahía San Carlos, ca. 28°10′N, 111°03.5′W, *R. Felger et al. 85-580* (ARIZ, CAS, MEXU, TEX); Loma Chomajabires, 1.8 mi N of Huatabampito, ca. 8 mi S of Huatabampo, 26°42′N,

109°36′W, *M. Fishbein & S. McMahon 2748* (ARIZ, CAS); vicinity of Nescotahueca, 4.5 km E of jct. of south Camahuiroa airstrip and Diez de Abril Road, 4 km W of Tierra y Libertad, 26°34′N, 109°15′W, *S. Friedman & G. Hall 398-93* (ARIZ); Arroyo Camahuiroa, 2 km NE of Camahuiroa, 9.5 km WNW of Melchor Ocampo, 26°33′N, 109°15.5′W, *S. Friedman & J. Zittere 025-95* (ARIZ); 277 km S of Nogales toward Hermosillo, *T. Frye & E. Frye 2283* (DS, GH, MO, NY, UC, US); N edge of Hermosillo, near Ganadero Motel, *A. Gentry 552* (MO); Cocorit, Yaqui Valley, *H. Gentry 885* (DS), *885M* (ARIZ); Salitral, Río Mayo, *H. Gentry 1291* (ARIZ, F); Cerro de Bavájori, 12 mi W of Navojoa, *H. Gentry 7953* (ARIZ, US); Algodones Bay, *D. Goldberg s.n.* (ARIZ); E end of bay at Port Libertad, *E. Graham 3810* (DS); 20 mi N of Port Libertad, *H. Green s.n.* (PH); ca. 30 mi S of Hermosillo on Hwy. 15, *B. Hansen et al. 1375* (MEXU, WIS); 2.1 mi NW of Bahía Kino, *J. Hastings & R. Turner 64-32* (ARIZ, DS); 2 mi N of Tastiota, *J. Hastings & R. Turner 65-168* (ARIZ); 3 mi SSE of Rancho Las Peñitas, 29.8°N, 111.8°W, *J. Hastings & R. Turner 69-112* (ARIZ); Islas Melisas in N part of Guaymas Bay, *J. Hastings et al. 61-39* (ARIZ); Punto Cirio, ca. 7 mi S of Puerto Libertad, *J. Hastings et al. 63-7* (ARIZ); "Catch 22" ca. 5 mi N of San Carlos, 27°57′N, 111°05′W, *A. Johnson 5013* (DAV); "Playas del Sol" ca. 10 mi S of Guaymas, 27°55′N, 110°45′W, *A. Johnson 5052* (DAV); Tiburón Island, Freshwater Bay, *I. Johnston 3250* (CAS); Tiburón Island, 3 mi N of Willards Point, *I. Johnston 4245* (CAS); 5 mi NW of Caborca on road to Tajitos, *D. Keck 4052* (C); 2 mi N of Horcasitas, *M. Kimnach & Lyons 596* (UC, US); 70 mi S of Hermosillo, *G. Lindsay 1133* (DS); Isla San Esteban, SE de la isla, *E. Lott & T. Atkinson 2458* (MEXU); 3 mi S of Mesquite, *F. Long 13* (US); Picu, *D. MacDougal & F. Shreve 15* (US); Kino Pt., *D. MacDougal & F. Shreve 27* (US); Arroyo Desemboque, 20 mi N of Sargento, *T. Mallery & W. Turnage s.n.* (DS); mouth of Salitral Creek at Río Mayo, Rancho Salitral near San Bernardo, *P. Martin 12* (ARIZ); 35 km SSW of Caborca on road to Libertad, ca. 30°28′N, 112°20′W, *P. Martin & S. Nilsson 9* (S); 7 km S of Libertad at Punta Cirio, ca. 29°50′N, 112°39′W, *P. Martin & S. Nilsson 13* (S); Estero Santa Barbara, W of Huatabampito, 26°42′N, 109°38′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); Sonoyta River, *E. Mearns 2790* (DS, NY, US); Sierra Seri, ca. 21°17′N, 112°08′W, *E. Moser et al. 18157* (ARIZ); Quitovac between Sonoyta and Caborca, *G. Nabhan et al. 249* (ARIZ); without locality, *E. Palmer s.n.* in 1869 (US); near Guaymas, *W. Palmer 1213* (US); 1/4 mi W of Condominios Pilar, 1 mi S of hwy. to San Carlos, ca. 4 mi W of Hwy. 15, *B. Parfitt & T. Reeves 2398* (ENCB); along Mex. Hwy. 8, near KM 19, S of US-Mexico border at Lukeville/Sonoyta, *L. Parker s.n.* (ARIZ); 6 mi N of Obregón, *K. Parker 8209* (ARIZ); 6 km WNW of San Carlos, 27°57′N, 111°06′W, *M. Quinn & P. Sudt 046* (ARIZ); 6.5 mi W of Río Yaqui along Hwy. 16 near La Barranca, ca. 28°28', 109°32′W, *A. Rea 1200* (ARIZ); Ensenada Chica, 15.1 mi W of Hermosillo to Guaymas Hwy. by dirt road, 6 mi S of San Augustin Beach turnoff, 28°07′N, 111°17′W, *F. Reichenbacher 230* (ARIZ); Mpio. San Pedro de la Cueva, Canada La Pila, 1 km N of Río Moctezuma, ca. 9.5 km NE of San Pedro de la Cueva, 29°18′N, 109°43′W, *A. Reina G. & T. Van Devender 99-255* (CAS); Mpio. Cd. Obregón, 0.5 km S of Estación Corral junction on Mex. 15 on road to Cocorit, 27°37′N, 109°58′W, *A. Reina G. & T. Van Devender 2001-178* (CAS); Mpio. Huatabampo, 6 km NW of Camahuiroa on road to Las Bocas, near Bachomojaqui, ca. 26°34′N, 109°18′W, *A. Reina G. et al. 98-2138* (MEXU); Mpio. Caborca, SE of Puerto Lobos, Ejido Manuel Avila Camacho, 30°16′N, 112°49′W, *A. Reina G. et al. 2000-166* (CAS); Mpio. Altar, Rancho El Rincón, 3.5 km S of Sásabe, 31°26′N, 111°34′W, *A. Reina G. et al. 2003-1291* (CAS); vicinity of Hermosillo, *J. Rose et al. 12374* (GH, NY, US); Kino Bay, *V. Rudd et al. 3042* (ENCB, MEXU); ca. 0.5 km S of Carnegie Peak, Sierra Pinacate, *N. Sakaki et al. 19881* (ARIZ, ENCB); Cañón del Coyote, ca. 4 mi NE of Desemboque, *C. Saravia T. s.n.* (ARIZ); near Port Libertad, *H. Shantz s.n.* (WIS); E trail of Pinacate Peak, 31°45′N, 113°30′W, *W. Sherbrooke s.n.* (ARIZ); inland from San Carlos Bay, Guaymas, *P. Sherwin 215* (DUKE); 5 mi NW of Caborca, *F. Shreve 7535* (ARIZ, F, MO); Cañón Palma, Sierra Libre, *F. Shreve s.n.* (MEXU); E of Pinacate Peak, Pinacate Mountains, *J. Soule s.n.* (ARIZ); Nacopuli Canyon, off road to San Carlos Bay, 28°01′N, 111°03.5′W, *G. Starr & C. Starr 204* (ARIZ); carretera Bahía Kino–Puerto Libertad, 40 km N de intersección con carretera a Hermosillo, 29°30′N, 112°15′W, *H. Suzán 315* (MEXU); Isla Tiburón, NW 20 km de la playa, Sierra Kunkaac, *F. Torres 4* (ENCB); Punto Cirio, ca. 6 mi S of Puerto Libertad, *R. Turner & C. Lowe 60-31* (ARIZ); ca. 12 mi S of Hermosillo, *T. Van Devender s.n.* (ARIZ); 29 mi S of Hermosillo on Hwy. 15, *T. Van Devender s.n.* (ARIZ); 3.2 mi S of Sásabe, *T. Van Devender s.n.* (ARIZ, GH, MEXU); Puerto Los Mochos, Rancho Los Mochos, ca. 20 mi NNE of Desemboque del Río San Ignacio on road to La Ciénega, *T. Van Devender & M. Kearns s.n.* (ARIZ, TEX); Sierra Bacha, Punto Cirio, near Libertad, *T. Van Devender & M. Kearns s.n.* (ARIZ); Mpio. Hermosillo, Cerrito de la Virgen, 5.4 km S of Hermosillo, 28°59′N, 110°58′W,

T. Van Devender & A. Reina G. 2004-2 (CAS); 8 km E of Tecoripa on MEX 16, ca. 28°37′N, 109°50′W, *T. Van Devender & A. Reina G. 2004-27* (CAS); 29.4 mi N of Hermosillo on Hwy. 15, *T. Van Devender et al. 88-838* (ARIZ); mouth of Arroyo Masiaca, Las Bocas on Gulf of California, ca. 52 km S of Navojoa, 26°36′N, 109°20′W, *T. Van Devender et al. 94-386* (ARIZ, CAS); Mpio. Navojoa, Teachive de Masiaca, Arroyo Masiaca, 26°47′N, 109°14′W, *T. Van Devender et al. 94-956* (ARIZ); Mpio. Hermosillo, Bahía de Kino, *T. Van Devender et al. 96-238* (ARIZ, MEXU); Sierra Bacha, SE of Punta Cirio, ca. 29°50′N, 112°37-38′W, *G. Webster 22457* (DAV, MEXU); near Ures, *J. Whitehead M152* (ARIZ); KM 101 on Hermosillo–Moctezuma road, 38.6 mi E of Moctezuma, ca. 29°28′N, 110°15′W, *A. Whittemore et al. 83-100* (CAS, MEXU, TEX); 2 mi W of Libertad, *I. Wiggins 6085* (DS, US); 10 mi N of Hermosillo, *I. Wiggins 6251* (DS, F, UC, US); 5 mi SE of Torres, *I. Wiggins 6286* (DS, UC, US); 17 mi NE of Cajeme toward Tesopaco, *I. Wiggins 6390* (DS, UC, US); 5.7 mi NW of Caborca toward Sonoyta, *I. Wiggins 8257* (DS, UC, US); Sierra Bacha, S of Punta Cirio, *F. Wiseman & W. Spaulding s.n.* (ARIZ).

Justicia candicans (Nees) L.D. Benson in L.D. Benson and R.A. Darrow, Trees and Shrubs of the Southwestern Deserts, ed. 3, 218. 1981. *Adhatoda candicans* Nees in A. de Candolle, Prodr. 11:396. 1847. *Dianthera candicans* (Nees) Hemsl., Biol. Cent.-Amer., Bot. 2:517. 1882. *Jacobinia candicans* (Nees) B.D. Jacks., Index Kew. 1:1246. 1893. TYPE: MEXICO. Oaxaca: "Cordillerae Mexicanae," 5000 ft., November–April 1840, *H. Galeotti 911* (holotype: K ex hb. Hook.!; isotypes: BR!, G!, P!, see discussion).

Jacobinia mexicana Seem., Bot. Voy. *Herald*, 325, t. 66. 1856. TYPE. MEXICO. State undetermined (see discussion): "Sierra Madre," *B. Seemann 2115* (lectotype, designated here, see discussion below: K ex herb. Hook.!).

Jacobinia ovata A. Gray, Proc. Amer. Acad. Arts 21:405. 1886. TYPE: MEXICO. Chihuahua: near Batopilas, Aug-Nov 1885, *E. Palmer 220* (holotype: GH!, photo at DS!; isotypes: G!, NY, US!).

Jacobinia ovata var. *subglabra* S. Wats., Proc. Amer. Acad. Arts 24:67. 1889. *Jacobinia candicans* var. *subglabra* (S. Watson) L.D. Benson in L.D. Benson and R.A. Darrow, Trees and Shrubs of the Southwestern Deserts, ed. 2, 413. 1954. *Justicia candicans* var. *subglabra* (S. Wats.) L.D. Benson in L.D. Benson and R.A. Darrow, Trees and Shrubs of the Southwestern Deserts, ed. 3, 218. 1981. TYPE: MEXICO. Sonora: rocky ravines, Guaymas, Oct 1887, *E. Palmer 264* (holotype: GH!; isotypes: C!, DS!, NY!, UC!, US).

Justicia mexicana Rose, Contr. U.S. Natl. Herb. 1:348. 1895. TYPE: MEXICO. Sonora: Agiabampo, 3-15 Oct 1890, *E. Palmer 788* (holotype: US!; isotypes: GH!, NY!, US!).

Phenology. Flowering: throughout the year, with peaks in March and November (Fig. 1); fruiting: September–April.

Distribution and habitats. Southwestern United States (Arizona), Mexico (Baja California Sur, Chihuahua, Colima, Durango, Guanajuato, Guerrero, Jalisco, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Sinaloa, Sonora); Sonoran plants occur on rocky slopes and along watercourses in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Plains of Sonora), palm oases, thornscrub, tropical deciduous forests, and grasslands at elevations from sea level to 1330 m.

Illlustrations. Figure 6; *The Botany of the Voyage of H.M.S.* Herald, t. 66. 1856; *Trees and Shrubs of the Southwestern Deserts*, 3rd. ed., 218. 1981; *Flora del Valle de Tehuacán-Cuicatlán* 23:53. 1999.

Local names. "Ciática" (fide Yetman and Van Devender 2002); "flor de chuparosa" (*Gentry 861*); "maso o'ota" (Mayo, *Van Devender et al. 93-1437*); "muicle cimarrón" (fide Van Devender et al. 2000); "palo de venado" (*Van Devender et al. 93-1437*); "rama venado" (*Van Devender et al. 93-1437*); "vipsumar" (Pima Bajo, *Rea 1262*).

Use. Yetman and Van Devender (2002) noted that the Mayo sometimes brew the leaves into a tea that is drunk as a treatment for malaria.

Locality data on the holotype of *Justicia candicans* at K is as noted above. The first set of Galeotti's collections is at BR, however, and locality information on the presumed isotype there indicates that the plants were collected in Tehuacán, Puebla at an elevation of 5250 ft. in August 1840. *Galeotti 911* at P indicates collection at 5000 ft. in Oaxaca but gives the date as August. Whether these collections represent duplicates of the same gathering in either Oaxaca or Puebla, or whether they represent different gatherings (and thus not duplicates) remains undetermined.

Based on information provided by McVaugh (1972), Seemann's type collection of *Jacobinia mexicana* was likely made in Sinaloa, Durango, or Nayarit. There are two specimens of *Seemann 2115* in Hooker's herbarium at Kew of about equal quality. The one selected as lectotype has original drawings on the sheet similar to those in the protologue. Plants of the type specimen have triangular bracteoles shorter than (i.e., not surpassing) the calyx thereby resembling the Gentry, Krizman & Soule, and Sanders et al. collections from Sonora noted below. *Jacobinia mexicana* was treated as a synonym of *Justicia candicans* by Daniel and Acosta (2003). By citing *Galeotti 911* under *Jacobinia mexicana* Hemsley (1882) also apparently felt that the types of *Jacobinia mexicana* and *Justicia candicans* represented the same taxon. Bentham and Hooker (1876) noted that "Adhatoda sericea Nees" was also a name that applied to *Jacobinia mexicana*; however, I can find no evidence that such a name was ever published by Nees.

Daniel (1997, 1999a) and Daniel and Acosta (2003) provided descriptions of *Justicia candicans*. The species is both widely distributed and morphologically variable. It occurs throughout much of Sonora (Fig. 23), but is especially common in regions of thornscrub and tropical deciduous forest. It occurs in three subdivisions of the Sonoran Desert, but is apparently very rare in the Arizona Upland and entirely absent from the Lower Colorado River Valley. In Sonora, some plants, especially some from near Guaymas, have stems and leaves either glabrous or very sparsely pubescent (e.g., *Brandegee s.n.*, *Felger & Thomas 11837*, *Palmer 264*, *Phillips et al. 75-152*). These have been treated taxonomically as *J. candicans* var. *subglabra*. Other plants, including the type of *Jacobinia ovata* from southwestern Chihuahua and several collections from Sonora (e.g., *Abrams 13218*, *Daniel 3348*, *Joyal 1562*, *Landrum et al. 5436*, *Wiggins 7151*) are densely and evenly pubescent with flexuose eglandular trichomes. Most Sonoran collections have a pubescence intermediate between these extremes. Because there appears to be a continuum in vegetative vesture from glabrous (or with very few trichomes) to densely pubescent, no formal taxonomic status is here accorded the various "pubescence forms" of this species. Few Sonoran plants of *J. candicans* show the well-developed clusters of cobwebby trichomes in axils of major veins on the abaxial surfaces of the leaves that were noted by Daniel and Acosta (2003) for representatives of the species in south-central Mexico. These are evident only in *Gentry 4879* and *Sanders et al. 4619*.

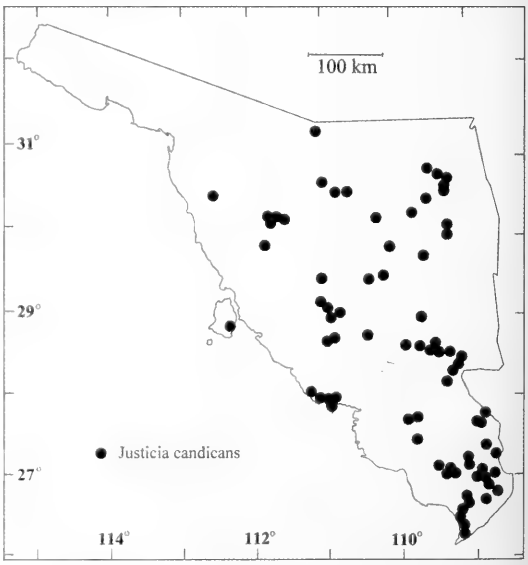


FIGURE 23. Sonoran distribution of *Justicia candicans*.

The types of *Jacobinia ovata, J. ovata* var. *subglabra*, and *Justicia mexicana* resemble the majority of Sonoran plants by having bracteoles lance-subulate to linear to oblanceolate and longer than (or overtopping) the calyx. Several specimens from Sonora (e.g., *Gentry 4879*, *Krizman & Soule s.n.*, and *Sanders et al. 4619*) have triangular to subulate to linear bracteoles that are shorter than the calyx. In this respect, they resemble the type of *Jacobinia mexicana*. Among the presumed type specimens of *J. candicans*, bracteoles vary in length from shorter than (or at least not surpassing) the calyx to equaling the calyx to slightly surpassing it and they vary in shape from lance-linear to linear to linear-elliptic. *Landrum et al. 5425* from Sonora also appears intermediate with its somewhat linear bracteoles that are slightly shorter than to nearly equal to the calyx. Because of the overlap in bracteolar form evident among plants occurring outside of Sonora, all of these plants are treated as comprising a single variable species.

The inflorescence of *Justicia candicans* consists of solitary dichasia in the leaf axils or of condensed dichasiate spikes in the leaf axils. The distal leaves bearing axillary inflorescences sometimes become reduced in size and bractlike, thereby resulting in a terminal, compound inflorescence. This is especially evident in *Felger 397*.

Sonoran collections: 6 mi S of Magdalena, *L. Abrams 13218* (DS); 12 mi NW of Hermosillo, *L. Abrams 13307* (DS); 3 km SSE of El Chinal Road toward Río Cuchujaqui, ca. 22.5 km SSE of Alamos, 26°51′N, 108°54′W, *M. Baker et al. 10371* (TEX); Hotel Playa, Guaymas, *R. Barr & W. Brewer 63-653* (ARIZ, MEXU); Cerro Bocochibampo, Guaymas, *E. Blakley B-1639* (DS); ca. 16 mi S and 6.5 mi W of Trincheras, 30.2°N, 111.6°W, *J. Bowers & R. Turner 2194B* (ARIZ); Guaymas, *T. Brandegee s.n.* (UC); San Javier, microondas on el Cerro El Durazno, 28°37′N, 109°45′W, *A. Búrquez 94-019* (MEXU); Cañón de Nacapule, Sierra el Aguaje, ca. 20 km N de Guaymas 28°01′N, 111°03′W, *A. Búrquez 94-251* (MEXU); 2.5 km S de Hermosillo, 29°01′N, 110°57′W, *A. Búrquez & A. Quijada 92-84* (MEXU); W of Magdalena, *O. Clark 12642* (GH); village 8 mi W of Torres, between Guaymas and Hermosillo, *F. Coville 1643* (US); "Microondas mountain" overlooking Guaymas, along road which is 1.8 mi from Mex. Hwy. 15 on paved road to airport, N of Guaymas, *T. Daniel 1957* (ASU); between Hwy. 16 E of Tonichi and Onavas, 0.5 mi S jct. Hwy. 16, *T. Daniel 3348* (CAS); Río Cuchujaqui, ca. 8 mi SE of Alamos, *T. Daniel & M. Butterwick 3192* (ASU, CAS); Nacapuli Canyon, 6.3 mi W of Hwy. 15 toward San Carlos, then 4.4 mi N, *T. Daniel et al. 1997* (ASU, CAS), *2336* (ASU, CAS); Mpio. Yécora, Arroyo La Quema, 0.3 km SE of Tepoca on Hwy. 16, ca. 28°26′N, 109°15′W, *T. Daniel et al. 8644* (CAS); Bahía San Carlos, *E. Dawson 1065* (DS); Magdalena, *F. Drouet & D. Richards 3810* (F, US); mountain on E side of Guaymas, *F. Drouet & D. Richards 3853* (F, US); Guaymas, *F. Drouet & D. Richards 3893* (F); mountain W of Alamos, *F. Drouet & D. Richards 3939* (F); Río de Sonora near Unión, Hermosillo, *F. Drouet et al. 3442* (F); 11 mi NE of Baviácora, *F. Drouet et al. 3663* (A, DS, F, MO, US); Palm Canyon, 25 km SSE of Magdalena on road to Cucurpe, 30°28′N, 110°48′W, *D. Ducote et al. 76-6* (ARIZ, MEXU-245739); near Navojoa, *C. Erlanson & M. Souviron 29* (US); Cañón de los Chapotes, E side of Sierra de Alamos, *R. Felger 397* (ARIZ, CAS, MEXU); Tiburón Island, Sierra Kunkaa, ca. 4 mi W of Punta Narragansett, SE part of island, *R. Felger 6972* (ARIZ, ENCB); Cerro Tetas de Cabra, Bahía San Carlos, *R. Felger 85-365* (ARIZ, MEXU); La Sorpresa, SW of Trincheras, ca. 30°10′N, 111°43′W, *R. Felger & A. Russell 6768* (ARIZ); Rancho San Jorge, W of Hermosillo, 29°44′N, 111°51′W, *R. Felger & A. Russell 6920* (ARIZ), *6943* (ARIZ); Cerro del Vigía, Guaymas, *R. Felger & R. Thomas 11837* (ARIZ, CAS, MEXU); 1.6 km W of Estero Solado, ca. 4.5 mi W of Mex. 15 on road to Bahía San Carlos, *R. Felger & D. Valdez Z. 84-541* (ARIZ); Ensenada Grande (= San Pedro Bay, north of San Carlos Bay), *R. Felger et al. 11576* (ARIZ, TEX); Cañón de Nacapules, ca. 6 km NE of Bahía San Carlos, *R. Felger et al. 84-92* (ARIZ, MEXU, TEX); El Novillo, *R. Felger et al. 84-232* (ARIZ); Arroyo Guajaráy, between Los Aguaros and Cajón del Ardilla, 27°39′N, 108°58′W, *R. Felger et al. 94-58A* (ARIZ); Cañón Las Barajitas, Sierra El Aguaje, ca. 18 km NW of San Carlos, ca. 28°03′N, 111°11′W, *R. Felger et al. 95-193* (ARIZ); El Reparo–Middle, old road to Bermudez, 28°21′N, 109°05′W, *G. Ferguson & C. Moore s.n.* (MEXU); ca. 8 mi N of Guaymas on San Carlos Bay, *R. Ferris 8724* (DS); 14.5 mi E of Río Yaqui on Mex. 16, *P. Fischer & G. Yatskievych 6887* (ARIZ); Rancho La Colorada, ca. 1.5 mi SW of Alamos, *J. Fish 189* (UC); 21 mi NE of Los Tanques at jct. with road to La Vinateria, 27°15′N, 108°42′W, *M. Fishbein et al. 96* (ARIZ); El Naranjo, Arroyo Taymuco,

27°15′N, 108°46′W, *M. Fishbein et al. 216* (ARIZ); N of Guaymas on Hwy. 15, *M. Fishbein et al. 221* (ARIZ); Mpio. Guaymas, Sierra El Aguaje, Aguaje Robinson, ca. 10 km NW de San Carlos, 28°03.5′N, 111°07′W, *A. Flores M. & O. Gutierrez R. 5089* (ARIZ, MEXU); Mpio. La Colorada, 4 km antes de San José de Pimas, carr. Hermosillo–Yécora, 28°46′N, 110°37′W, *A. Flores M. & J. Sánchez E. 4871* (ARIZ, MEXU); Mpio. Hermosillo, La Pintada, 50 km S de Hermosillo, 28°35′N, 110°58′W, *A. Flores M. & J. Sánchez E. 5452* (IEB); 9.5 km S on Mex. 15 from Las Bocas Road turnoff, 3.5 km W on Sirebampo Road, 11.5 km S of San José de Masiaca, 26°39′N, 109°15′W, *S. Friedman & J. Zittere 90-95* (ARIZ); 9.8 km W of Mex. 15 on Las Bocas Road, 37 km SE of Huatabampo, 5.6 km E of Las Bocas, 26°39′N, 109°19.5′W, *S. Friedman & J. Zittere 149-95* (ARIZ); Distr. Alamos, Quiricoba, *H. Gentry 743* (DS); Distr. Alamos, Cuchuhacki Arroyo, *H. Gentry 861* (DS); Agua Caliente, Distr. Alamos, *H. Gentry 905M* (ARIZ); Canyon Sapopa, Río Mayo, *H. Gentry 1029* (ARIZ, MO, US); Caramechi, Río Mayo, *H. Gentry 1206* (A, ARIZ, F, MEXU, MO, WIS, S, UC, US); near Las Guásimas, Navojoa–Alamos road, *H. Gentry 4879* (ARIZ, MEXU, MO); Los Cerritos, ca. 40 mi N of Navojoa, *H. Gentry 14393* (ARIZ, US); Sierra Bojihuacame SE of Cd. Obregón, *H. Gentry 14499* (ARIZ, LL, US); Ures, *D. Gold 756* (MEXU, MO); ca. 6 mi W of Santa Ana de Yécora, *D. Goldberg 77-78* (ARIZ); 4.3 km SW of Santa Ana de Yécora, 28°23′N, 109°19′W, *D. Goldberg & R. Frye 77-271* (ARIZ); Las Cuevas, *C. Hartman 159* (GH); Oputo, *C. Hartman 211* (A, GH, PH, US); 11 mi S of Nacozari, *J. Hastings & R. Turner 65-110* (ARIZ); Lo de Campo Ranch, 6 km S of San Javier on Río San Javier, S of Hwy. 16, 28°32.1′N, 109°44.6′W, *P. Holm s.n.* (ARIZ); Mpio. Alamos, Río Cuchujaqui, 27°02′N, 108°42′W, *P. Jenkins 89-430* (ARIZ); Santa Ana de Yécora, *P. Jenkins s.n.* (ARIZ); Guaymas, *I. Johnston 3095* (CAS); San Pedro Bay, *I. Johnston 4312* (CAS); Guaymas, *M. Jones 23264* (CAS, MO, UC); between cerros El Cucurucho and El Aguaje from Alamos to La Higuera, 27°04–05′N, 108°58′W, *E. Joyal 1344* (CAS, MEXU, TEX); Puenta La Pila, above "El Palmar," ca. 20 km E of Onavas, 28°29′N, 109°22′W, *E. Joyal 1562* (CAS, MEXU); 1 mi E of Navojoa, *R. Kirzman & O. Soule s.n.* (ARIZ); road to Sahuaripa, ca. 22 mi E of Hwy. 15 bypass, *L. Landrum et al. 5425* (CAS); 2.6 mi E of bridge at Huásabas, *L. Landrum et al. 5436* (CAS, GH); Arroyo Gochico, ca. 8 km E of San Bernardo, 27°24′N, 108°47′W, *G. Levin et al. 2018* (CAS); Tres Marias limestone quarry, 27°07′N, 109°10′W, *P. Martin s.n.* (ARIZ, C); 8 km E of Alamos on road to Sabinito Sur, *P. Martin & G. Ferguson s.n.* (ARIZ); Cerro Verde, 28°34′N, 109°44′W, *P. Martin & G. Ferguson s.n.* (ARIZ); Puerto El Chino, 26°41.3′N, 108°57.8′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); Guaymas, Microwave Mountain, 27°57′N, 110°54′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); NE of Alamos toward Cuchujaqui, 27°01–06′N, 108°53–55′W, *P. Martin et al. s.n.* (ARIZ, CAS); Estación Margarita, 10 km NW of Navojoa, *P. Martin et al. s.n.* (ARIZ); Jorinabo, along Río El Naranjo, 27°15.5′N, 108°46.4′W, *P. Martin et al. s.n.* (ARIZ); Palm Canyon, 17 mi SE of Magdalena on road to Cucurpe, Sierra Baviso, *N. McCarten & R. Bittman 2712* (ARIZ); 30 mi N of Nuri, *S. McLaughlin & M. Karpiscak 518* (ARIZ); Río Yaqui drainage, Cerro Verde to San Javier, 28°35′N, 109°44′W, *K. Moore s.n.* (ARIZ, CAS); San Pedro Bay, 28°03.5′N, 111°17′W, *R. Moran 4038* (DS, UC); Mpio. Guaymas, Cañón Los Anegados, ca. 2.8 km del Rancho El Aguaje de Robinson, 28°02′N, 111°08′W, *L. Moreno M. et al. 41* (ARIZ); Río Moctezuma, 10 mi SW Nacozari, 30°15′N, 109°40′W, *T. Nash et al. L19447* (CAS, US); ca. 43 mi N of Guaymas along Hwy. 15 near microwave station, *D. Norris et al. 20041* (DS, MEXU, MO); 6 mi W of Nuri on road to Movas, *M. O'Rourke & P. Martin s.n.* (ARIZ); Guaymas, *E. Palmer 264* (US); Mpio. Hermosillo, Predio Ranchito de la Sierra, *A. Peinado et al. A-05* (MEXU); S of Magdalena, *F. Pennell 20265* (PH); Nacopuli Canyon, 3.5 mi N of San Carlos Bay, *A. Phillips et al. 75-152* (ARIZ, UC); region of Río Bavispe, Valle de Teras, *E. Phillips 755* (GH); Onavas, ca. 28°28′N, 109°32′W, *A. Rea 1262* (ARIZ); 2.3 mi E of Río de Bavispe by Huásabas to El Coyote and Huachinera Road, 29°56′N, 109°16′W, *F. Reichenbacher 216* (ARIZ); Palm Canyon, 15.5 mi toward Cucurpe from Mex. 15 in Magdalena, *F. Reichenbacher 913* (CAS); 2 mi E of Santa Rosa and 17 mi W of Yécora, *F. Reichenbacher & L. Toolin 1373* (ARIZ); Mpio. Moctezuma, Río Moctezuma at San Clemente de Terapa, 29°41′N, 109°39′W, *A. Reina & T. Van Devender 2003-576* (CAS); Mpio. Soyopa, vicinity of Río Yaqui bridge on Mex. 16, just S of Tonichi, ca. 28°34′N, 109°33′W, *A. Reina et al. 97-09* (ARIZ); Mpio. Nacozari de Garcia, Rancho Agua Caliente (Río Bavispe drainage), 23.2 km SE of Esqueda, 30°39′N, 109°25′W, *A. Reina G. et al. 2004-376* (CAS); Guaymas, *H. Ripley 14294* (CAS); vicinity of Hermosillo, *J. Rose et al. 12481* (F); Sierra de Alamos, *J. Rose et al. 12780* (NY, US); Mpio. Alamos, vic. of Presa Mocuzari, 27 km SW of Alamos, ca. 27°14′N, 109°05′W, *A. Sanders & G. Helmkamp 13319* (CAS); N end of Sierra El Viejo, 25 mi SW of Caborca, ca. 30°22′N, 112°22′W, *A. Sanders et al. 3530* (ARIZ); near Mina Sahuarito, 20 mi

SW of Trincheras, ca. 30°09′N, 111°43′W, *A. Sanders et al. 3582* (ARIZ, CAS, UC); Cerro Prieto (= Cerro Colorado), near summit, 8.6 mi E of Navojoa toward Alamos, ca. 27°15′N, 109°17′W, *A. Sanders et al. 4619* (CAS); near Santa Rosa, 25 mi S of Trincheras, *F. Shreve 6049* (ARIZ, F); 37 mi NE of Cajeme on road to Tesopaco, *F. Shreve 6153* (ARIZ, MEXU); 7 mi S of Magdalena, *F. Shreve 10039* (ARIZ); La Pintada Canyon, Hwy. 15, 32.5 mi S of Hermosillo, *E. Smith 3973* (CAS, MEXU, TEX); Palm Canyon, 17.7 mi SE of Magdalena, road to Curcupe, Cerro Cinta de Plata, 30°29′N, 110°48′W, *G. Starr & K. Birgy 157* (ARIZ); 1.8 mi E of Alamos on road to Guadalupe, 27°02′N, 108°54.5′W, *G. Starr & D. Palzkill 317* (ARIZ); Cerro Dos Negritos, 1.8 mi N of Alamos, 27°03′N, 108°56′W, *G. Starr & D. Palzkill 380* (ARIZ); Microondas hill, Guaymas, *G. Starr & C. Starr 196* (ARIZ); Nacopuli Canyon, 28°01′N, 111°03.5′W, *G. Starr & C. Starr 205* (ARIZ); Canyon de la Bota, N end of Sierra El Tigre, ca. 36 mi E of Esqueda, ca. 30°36′N, 109°13′W, *G. Starr et al. 31* (ARIZ); Mpio. de Alamos, Sierra de Alamos along Arroyo El Huirotal, ca. 26°57′N, 108°57′W, *V. Steinmann 1295* (CAS); Cerro La Salada, 29.4°N, 111.0°W, *R. Turner & D. Brown 85-131* (ARIZ); Bahía San Pedro, 28.1°N, 111.2°W, *R. Turner et al. 79-292* (ARIZ); Sierra Alamos, ca. 4 mi SSW of Alamos, 26°59′N, 108°57′W, *R. Van Devender & T. Van Devender 83-126* (ARIZ); 5.2 mi ENE of Cucurpe on road to Rancho Agua Fria, *T. Van Devender s.n.* (ARIZ); 17 mi SE of Magdalena in Sierra Babiso (= Cerro Cinta de Plata), *T. Van Devender s.n.* (TEX); 8.2 mi E of Restaurante La Pintada on Mex. 15, Cañón La Pintada, Sierra Libre, *T. Van Devender s.n.* (ARIZ); Cañón Babiso, Rancho Babiso, 2.5 mi W of San Carlos Bay, *T. Van Devender & M. Kearns s.n.* (ARIZ); Palm Canyon, Cerro Cinta de Plata, 17.7 mi SE of Magdalena, *T. Van Devender & C. Miksicek s.n.* (ARIZ); Playa La Manga, N of San Carlos Bay, *T. Van Devender & F. Nishida s.n.* (ARIZ); 8.7 km E of Tecoripa on MEX 16, 28°37′N, 109°48′W, *T. Van Devender & A. Reina G. 2004-26* (CAS); ca. 8 mi E of turnoff of Son. Hwy. 12 at Esqueda on road to El Tigre, 30°39′N, 109°25′W, *T. Van Devender et al. 82-32a* (ARIZ); Cañón de la Bota, N end of Sierra El Tigre, ca. 34 km ESE of Esqueda, ca. 30°36′N, 109°13′W, *T. Van Devender et al. 82-52* (ARIZ); Guaymas Microwave Tower road (Microondas El Vigia), *T. Van Devender et al. 84-227* (ARIZ); El Guayabo crossing of Río Cuchujaqui, 2.6 km NE of Sabinito Sur, 14 km ESE of Alamos, 27°00′N, 108°47′W, *T. Van Devender et al. 92-1265* (ARIZ); 8.9 mi ESE of Alamos, Río Cuchujaqui, 26°59′N, 108°49′W, *T. Van Devender et al. 92-1333* (ARIZ); El Rancheria crossing of Río Cuchujaqui, ca. 22.5 km S of Alamos toward El Chinal, 26°51′N, 108°55′W, *T. Van Devender et al. 93-29* (ARIZ, CAS); Mocuzari Dam on Río Mayo, 27°13′N, 109°07′W, *T. Van Devender et al. 93-223* (ARIZ, CAS, MO, TEX); canyon N of Los Aguaros on Arroyo Guajaray, 27°38.5′N, 108°58′W, *T. Van Devender et al. 93-490* (ARIZ, in part); Laguna Barochipa, ca. 3.3 km SSE of Camahuiroa, 26°31′N, 109°16′W, *T. Van Devender et al. 93-1272* (ARIZ, CAS); Saucito Canyon, Rancho La Sierrita, 6 km SSW of Alamos, 26°58.5′N, 108°58′W, *T. Van Devender et al. 93-1366* (ARIZ, CAS); Mpio. Alamos, Cerro El Chorro, 4 km NW of Yocogigua, 26°49′N, 109°03.5′W, *T. Van Devender et al. 93-1437* (ARIZ, CAS); El Rincon Viejo, ca. 4 km N of Alamos, Sierra de Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 93-1509* (ARIZ); 4.3 km SW of Huasaguari on Masiaca–San Antonio de Las Ibarras road, 26°47.5′N, 109°11′W, *T. Van Devender et al. 95-275A* (ARIZ, TEX); 1.5 km SW of Santa Ana on road to Guadalupe Tayopa, 28°23′N, 109°09.5′W, *T. Van Devender et al. 97-213* (ARIZ, MEXU); Ejido Francisco Solis, 7 km ENE of Est. Luis (SE of Navojoa on Mex. 15), 26°35′N, 109°06′W, *T. Van Devender et al. 98-2113* (MEXU); Mpio. Nogales, 3.8 km NE of El Correo (La Arizona), Rancho Las Boregas, Arroyo Planchas de Plata, 31°11.5′N, 111°10′W, *T. Van Devender et al. 2004-214* (CAS); 20.4 mi SE of Magdalena on Cucurpe road, *T. Van Devender et al. s.n.* (ARIZ); E of Restaurante La Pintada (ca. 78 km N of Guaymas on Mex. 15), Cerro Bola in Sierra Libre, *T. Van Devender et al. s.n.* (ARIZ); 3.9 mi SW of Mazocahui, *T. Van Devender et al. s.n.* (ARIZ); San Javier, puerto San Juan a 1.5 km S del poblado, 28°35′N, 109°45′W, *L. Varela & E. Cuamea 97-7* (MEXU); near Bahía San Carlos, W of Guaymas, ca. 27°57′N, 111°04′W, *G. Webster 19725* (ARIZ, MEXU); 39 mi E of San José de Pimas, 28°38′N, 110°00′W, *G. Webster 23808* (MEXU); Cañada Motepori, ca. 9 mi NW of Banamichi crossing, ca. 30°04′N, 110°20′W, *G. Webster & R. Murphey 21475* (ARIZ, GH, MEXU); above Aduana, Sierra de Alamos, 8 km ESE of Alamos, 27°02′N, 109°02′W, *J. Weins et al. 93-092* (ARIZ, CAS); 2 mi E of Rancho San Carlos, on road to Norio, *I. Wiggins 6142* (DS); 23 mi NE of Cajeme on road to Tesopaco, *I. Wiggins 6402* (DS, UC, US); E of La Palma, 5 mi N of Guaymas in Sierra Libres, *I. Wiggins 6478* (DS, F, UC, US); SW side of Babiso Mts., 18 mi SE of Magdalena, *I. Wiggins 7151* (A, ARIZ, DS, UC, US); N of Los Aguaros on Arroyo Guajaray, 27°38′N, 108°58′W, *D. Yetman et al. s.n.* (CAS).

Justicia caudata A. Gray, Proc. Amer. Acad. Arts 21:405. 1886. TYPE: MEXICO. Chihuahua: near Batopilas, Aug-Nov 1885, *E. Palmer 189* (holotype: GH!; isotypes: K!, US).

Phenology. Flowering: March–April, August–November; fruiting: March–April, September–November.

Distribution and habitats. Mexico (Chihuahua, Chiapas, Distrito Federal, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, Sinaloa, Sonora, Zacatecas), Guatemala; Sonoran plants occur on rocky slopes, along watercourses, and in disturbed areas in tropical deciduous forests and oak woodlands at elevations from 240 to 805 m.

Illustration. *Flora Fanerogámica del Valle de México*, 716. 2001.

Daniel (1995a, 1999a) and Daniel and Acosta (2003) provided descriptions of *Justicia caudata* and discussed some of its variation. The species reaches its northwestern distributional limit in east-central Sonora (Fig. 24). Plants from Sonora are rather homogeneous with the young stems usually sparsely pubescent with retrorse or downward pointing (rarely flexuose) eglandular trichomes 0.2–1 mm long, the abaxial surfaces of the petioles conspicuously glandular pubescent, and the corollas pink-purple with white markings on the lower lip and 18–31 mm long.

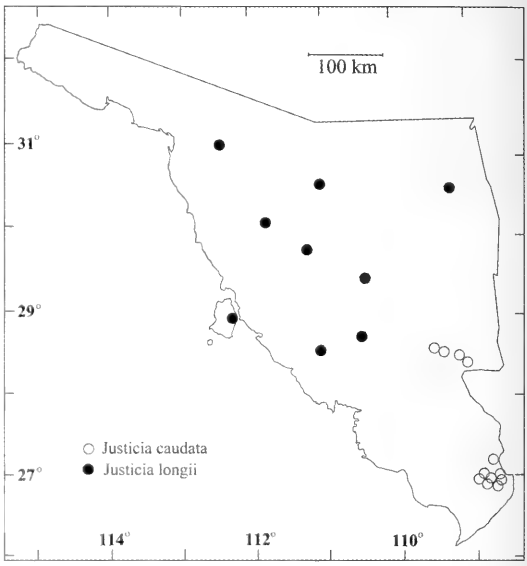


FIGURE 24. Sonoran distributions of *Justicia caudata* and *J. longii*.

SONORAN COLLECTIONS: ca. 3 km N de Tepoca sobre Mex. 16, 28°27′N, 109°16′W, *A. Búrquez M. 94-138* (CAS); southeastern border of Alamos (road to mirador), ca. lat. 27°01′N, long. 108°56′W, *T. Daniel 9771* (CAS); Río Cuchujaqui, ca. 8 mi SE of Alamos, *T. Daniel & M. Butterwick 3195* (CAS); Alamos area, road to Río Cuchujaqui, *A. Faivre et al. 64* (ARIZ); Arroyo La Barranca de Tonichi, 8.1 mi E of Río Yaqui along Hwy. 16, *M. Fishbein et al. 2448* (ARIZ); 4.3 km SW of Santa Ana de Yécora on road to Nuri, 28°23′N, 109°19′W, *D. Goldberg & S. McLaughlin 77-178* (ARIZ, TEX); Río El Naranjo crossing N of Taymuco, 27°15′N, 108°43′W, *P. Jenkins & P. Martin 88-252* (ARIZ); Mpio. Alamos, upper Río Cuchujaqui, Palmarito Canyon, 27°04′N, 108°45′W, *P. Jenkins et al. 92-82* (ARIZ); Rancho las Uvalamas near Alamos, 26°58′N, 108°55–56′W, *P. Martin & M. McWhorter s.n.* (ARIZ, CAS); Arroyo el Mentidero at El Chinal road, 11.3 km S of Alamos, 26°55′N, 108°55′W, *S. Meyer s.n.* (CAS); Alamos, *E. Palmer 402* (US); 2.5 mi W and 3/4 mi S of Alamos, *R. Perrill & V. Phelps 5168* (ARIZ); 12 km E of Alamos toward upper crossing of Río Cuchujaqui, ca. 27°00′N, 108°50′W, *A. Sanders et al. 9423* (ARIZ, CAS, TEX); Mpio. Alamos, Arroyo Mentidero, from Alamos–El Chinal road to Río Cuchujaqui, 12 km S of Alamos, 26°55′N, 108°55′W, *A. Sanders et al. 12575* (CAS, MEXU); 1 km W of Son. 12 on road to La Quema, 28°22′N, 109°16′W, *T. Van Devender & A. Reina G. 97-1029* (ARIZ, CAS, MEXU, TEX); Mpio. Yécora, Arroyo El Pilladito, near Tepoca, 28°26′N, 109°15′W, *T. Van Devender & A. Reina G. 98-1058* (CAS, MO); Mpio. Yécora, ca. 1.5 km SE of San Nicolas on Mex. 16, *T. Van Devender & A. Reina G. 2000-670* (MO); Arroyo El Cobre, near Choquincahui, 26°59′N, 108°41′W, *T. Van Devender & D. Yetman 94-741* (ARIZ); Arroyo Guirocoba, 2.3 km NE of El Cajón de Sabino, 4.8 km S of Guirocoba, 26°51.5′N, 108°42′W, *T. Van Devender & D. Yetman 94-763* (ARIZ); Arroyo el Mentidero at El Chinal road, 11.3 km S of Alamos, 26°55′N, 108°55′W, *T. Van Devender et al. 92-968* (ARIZ), *93-838* (ARIZ, CAS); El Guayabo crossing of Río Cuchujaqui, 2.6 km NE of Sabinito Sur, 14 km ESE of Alamos, 27°00′N, 108°47′W, *T. Van Devender et al.*

92-1224 (ARIZ); El Rincon Viejo, ca. 4 km N of Alamos, Sierra de Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 94-625* (ARIZ, TEX).

Justicia hilsenbeckii T.F. Daniel, nom. nov.

Siphonoglossa mexicana Hilsenb., Madroño 36:198. 1989. TYPE: MEXICO. Sinaloa: Imala, 29 Nov 1939, *H. Gentry 5099* (holotype: CAS!; isotypes: GH, MO, NY, US), non *Justicia mexicana* Rose (1895).

Phenology. Flowering: December; fruiting: December.

Distribution and habitats. Endemic to Mexico (Durango, Guerrero, Jalisco, Michoacán, Morelos, Puebla, Sinaloa, Sonora, and Veracruz); Sonoran plants occur in tropical deciduous forests at an elevation of 500 m.

Illustration. *Madroño* 36:199. 1989.

Local name. "Cordoncillo" (fide Yetman and Van Devender 2002).

Use. The Mayo make a tea from the branches that is used as a wash for rheumatism (Yetman and Van Devender 2002).

A description of this species, as *Siphonoglossa mexicana*, was provided by Hilsenbeck (1989). Daniel (1995a, 1999b) noted that this species, as well as other species of *Siphonoglossa* recognized by Hilsenbeck (1989, 1990a), would appear to be best treated in *Justicia*. Graham (1988) also included the type of *Siphonoglossa* within *Justicia*. A new name is necessary for *S. mexicana* when it is treated in the latter genus. The distinctions among *J. canybi* Greenm., *J. ramosa* (Oerst.) Graham, and *J. hilsenbeckii* do not appear to be substantial. Indeed, Hilsenbeck (1989) noted overlap in morphological traits between *J. canbyi* (as *S. canbyi* (Greenm.) Hilsenb.) and *J. hilsenbeckii* (as *S. mexicana*) and between *J. ramosa* (as *S. ramosa*) and *J. hilsenbeckii* (as *S. mexicana*). As a result, plants treated by Hilsenbeck as *S. mexicana* exhibit considerable variation in many quantitative characters and in pubescence. The entire complex warrants thorough restudy from throughout its range. Morphological data used above in the key to species of *Justicia* in Sonora is derived from the only known Sonoran collection and the type, which greatly resemble one another. The species reaches the northern extent of its distribution in southern Sonora (Fig. 22).

Among Sonoran Acanthaceae, this species might be confused with the morphologically similar one, *J. sonorae*. Sonoran representatives of these two species can be distinguished by the following couplet:

1. Corolla (15–) 19–24 mm long, tube cylindric (expanded only near mouth), 11–19 mm long, 0.6–0.8 mm in diameter at midpoint, lower lip 4–6.5 mm long; thecae 0.9–1.2 mm long, unequally inserted (overlapping by 0.6–0.8 mm); capsule 7–10 mm long. . . . . *J. hilsenbeckii*
1. Corolla 23–35 mm long, tube gradually expanded from near base to apex, 18–23.5 mm long, 1.8–2.7 mm in diameter near midpoint, lower lip 8–17 mm long; thecae 1.2–2.2 mm long, subequally inserted (overlapping by 1–1.5 mm); capsule 10–13.5 mm long. . . . . *J. sonorae*

Sonoran collection: Sierra de Alamos, El Rincón Viejo, Arroyo El Aguaje, ca. 4 km N of Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 93-1508* (ARIZ, CAS).

Justicia longii Hilsenb., Pl. Syst. Evol. 169:231. 1990. *Siphonoglossa longiflora* (Torr.) A. Gray, Syn. Fl. N. Amer. 2(1): 328. 1878. *Adhatoda longiflora* Torr. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):125. 1859, non *Justicia longiflora* Vis. (1839, 1840). TYPE: MEXICO. Sonora: road between Zuñi and Altar, Sep 1855, *A. Schott III no. 3 (Mex. Bound. Surv. 726)* (holotype: NY!; isotypes: F!, US).

Perennial herbs to 3.5 (–8) dm tall. Young stems subquadrate to multi-striate, evenly pubescent with retrorse to retrorsely appressed eglandular trichomes 0.05-0.8 mm long. Leaves subsessile to petiolate, petioles to 10 mm long, blades linear-lanceolate to lanceolate to elliptic to ovate, 5–70 mm long, 2–12 (–18) mm wide, 2–10 times longer than wide, (rounded to) acute to acuminate to subfalcate at apex, acute to subattenuate at base, surfaces pubescent with mostly antrorse eglandular trichomes 0.05-0.8 mm long, trichomes sometimes becoming restricted to major veins on mature leaves. Inflorescence of axillary sessile to subsessile (i.e., borne on peduncles to 1 mm long) dichasia; dichasia opposite at distal leaf nodes, 1 per axil, 1–3 (or more)-flowered. Bracteoles often subfoliose, linear to lance-elliptic, 4–24 mm long, 0.5–4.7 mm wide, abaxial surface pubescent like leaves; secondary bracteoles, if present, usually similar to bracteoles except smaller (sometimes becoming ± subulate). Flowers sessile. Calyx 5-lobed, 4–9 (–12) mm long, lobes linear to lance-elliptic, 3.5–8 (–10.5) mm long, 0.7–2.1 mm wide, narrowed proximally (i.e., widest above base), abaxially puberulent with antrorse eglandular trichomes 0.05 mm long. Corolla entirely white, 31–55 mm long, externally pubescent with flexuose to retrorse eglandular trichomes 0.1–0.3 mm long, tube cylindric, 23–43 mm long, 1–1.5 mm in diameter near midpoint, upper lip 5–12 mm long, 2-lobed at apex, lobes 0.5–1 mm long, 0.8–1.2 mm wide, lower lip 6–13 mm long, lobes 4–12 mm long, 3–5.6 mm wide. Stamens 4–7 mm long, filaments glabrous; thecae 1–2 mm long (including basal appendage), equal to subequal in size, parallel to subparallel, unequally inserted (overlapping by 0.6–1 mm), glabrous, both with a basal appendage or the upper theca lacking an appendage, basal appendages 0.2–0.3 mm long; pollen (Fig. 21) 3-aperturate, apertures flanked on each side by 2 (–3) rows of insulae. Style (23–) 32–41 mm long, pubescent with eglandular trichomes, stigma 0.2–0.3 mm long, subhemispheric to ± equally 2-lobed. Capsule 6.5–10 mm long, glabrous, stipe 2.5–4 mm long, head ovoid to ellipsoid to subglobose. Seeds 4, lenticular, 2–2.7 mm long, 2–2.5 mm wide, surface and margin bubbly-tuberculate.

Phenology. Flowering: March, August–December; fruiting: March, September–December.

Distribution and habitats. Southwestern United States (Arizona, Texas), northwestern Mexico (Sonora); Sonoran plants occur on rocky slopes in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Plains of Sonora) and thornscrub at elevations from 380 to 910 m.

Illustrations. Figure 25; *Plant Systematics and Evolution* 169:228. 1990.

In the protologue of *Adhatoda longiflora* Torrey cited: "road between Zuñi and Alta Sonora, September; *Schott*." Hilsenbeck annotated the sole specimen in Torrey's herbarium at NY with this information as the lectotype. It is here regarded as the holotype. On a sheet at F, there are four Schott labels (road between Zuñi and Altar, 1855, III.3.; near Pozo de Marias, no date, no number; Sta. Magdalena, no date, 1; near Sta. Gertruda del Altar, no date, no number) and seven shoots (all pertaining to *J. longii*), but with no correlation of labels and shoots. Hilsenbeck annotated the "specimen" as an isolectotype of *Adhatoda longiflora*. Because at least one of these labels agrees with information on what is here considered to represent the holotype at NY, an isotype is present among the various collections on this sheet.

Although Hilsenbeck (1990b) provided a recent description of *Justicia longii*, his circumscription of the species included *J. masiaca* as well. Thus, a description of *J. longii* based on plants from throughout its range is provided here. The species is nearly endemic to the Sonoran Desert region and reaches the southern limit of its distribution in central Sonora (Fig. 24). Because the species has been collected in Chihuahuan desertscrub in western Texas, it should be sought in the isolated region of that community in northeastern Sonora.

The distinctions between *J. longii* and *J. masiaca* are apparently all associated with the flowers; as a result, non-flowering collections can be difficult to identify. For example, *Daniel 981* lacks flowers and is tentatively treated as the former species primarily on the basis of the location where

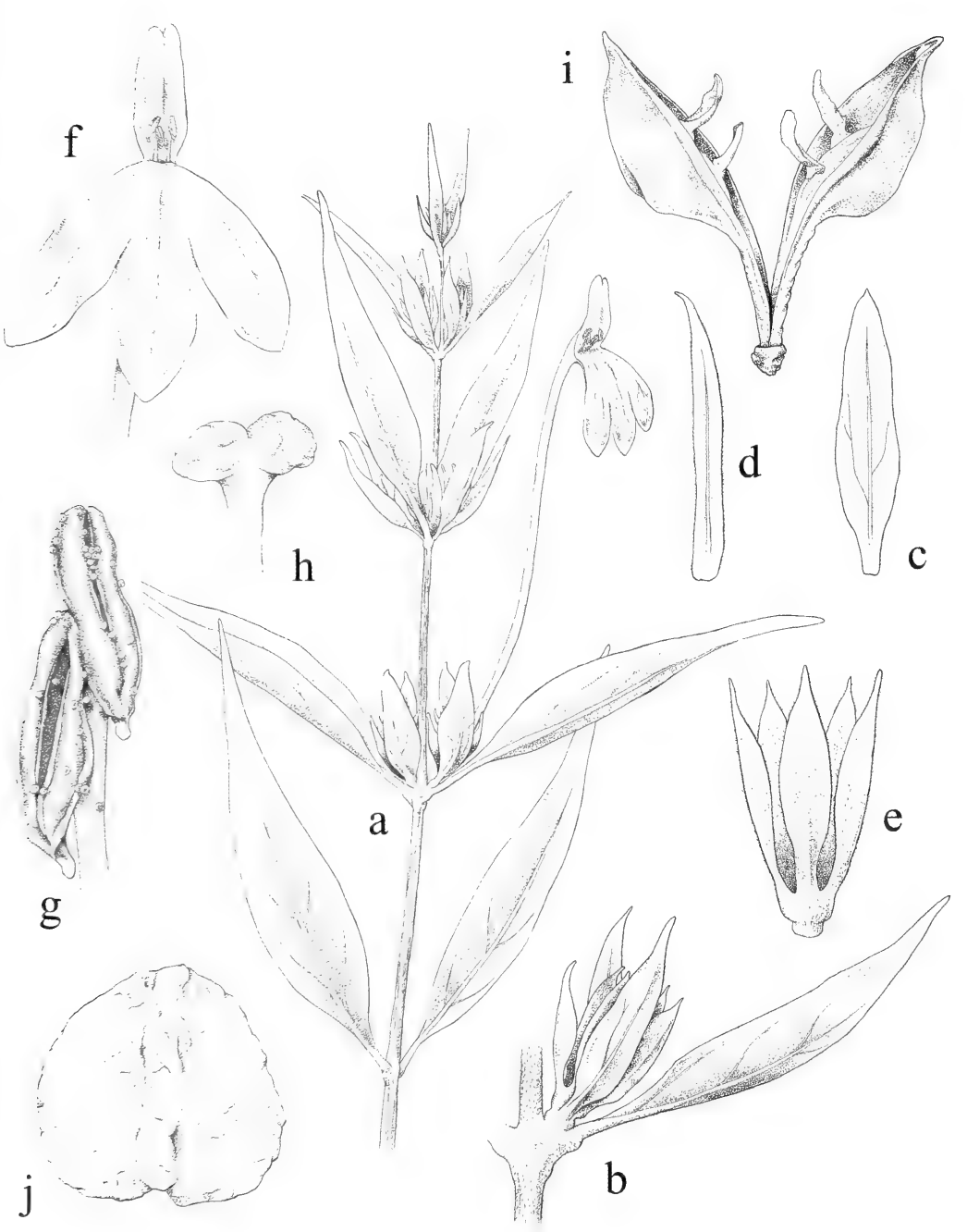


FIGURE 25. *Justicia longii*. a. Habit (*Jenkins & McLaughlin 1016*), ×1.2. b. Node (*Daniel 159*), ×4.5. c. Bracteole (*Jenkins & McLaughlin 1016*), ×2.7. d. Secondary bracteole (*Jenkins & McLaughlin 1016*), ×5.6. e. Calyx (*Turner et al. 78-45*), ×5.6. f. Distal portion of corolla and stamens (*Jenkins & McLaughlin 1016*), ×1.9. g. Anther (*Butterwick & Hillyard 7384*), ×29. h. Stigma (*Gould et al. 2799*), ×42. i. Capsule (*Daniel 159*), ×5.9. j. Seed (*Daniel 119*), ×15. Drawn by Alan Chou.

it was collected (which is nearer to populations of *J. longii* than to those of *J. masiaca*).

Sonoran collections: between La Colorada and Tecoripa, 12.6 mi E of La Colorada, *T. Daniel 981* (CAS); Isla Tiburón, NE [NW fide Felger, pers. comm.] of Santa Rosa, *R. Felger 9349* (ARIZ, MEXU); S end of Sierra Libre, 12.3 mi S of La Palma on Hwy. 15 (at KM 190), then 4.9 mi E of Hwy. to 0.1 mi below summit of Microondas Avispas, 28°29′N, 111°02′W, *R. Felger & F. Reichenbacher 85-1099* (ARIZ, MEXU, TEX); La Sorpressa, SW of Trincheras, 3010′N, 11143′W, *R. Felger & A. Russell 6756* (ARIZ); 12.3 mi W of Mex. 15 on Tecolote Road (1.2 mi N of El Oasis), 29°47′N, 111°15′W, *R. Reichenbacher 1060* (ARIZ); Mpio. Ures, 4 km NNW of Ures on road to Rayón, Río Sonora drainage, 29°27′N, 110°25′W, *A. Reina G. & T. Van Devender 2001-07* (ARIZ, MEXU, CAS); Mpio. Nacozari de García, Rancho Agua Caliente (Río Bavispe drainage), 23.2 km SE of Esqueda, 30°39′N, 109°25′W, *A. Reina G. et al. 2004-379* (CAS); near Mina Sahuarito, S of Cerro San Luis on road from Mina San Ignacio, 20 mi SW of Trincheras, ca. 30°09′N, 111°43′W, *A. Sanders et al. 3583* (ARIZ, CAS, UC); 7 mi S of Magdalena, *F. Shreve 6657* (ARIZ); 36 mi NW of Caborca and 16.5 mi NW of Tajitos, 31.2°N, 112.5°W, *R. Turner & J. Hastings 72-36* (ARIZ, MEXU); between Magdalena and Santa Ana, 7 mi S of Magdalena, *I. Wiggins 7190* (DS, F, GH, MICH, UC, US).

Justicia masiaca T.F. Daniel, Brittonia 47:408. 1995. TYPE: MEXICO. Sonora: between Masiaca and Alamos, 1.6 mi NE of Masiaca and 7.1 mi NE of Hwy. 15, ca. 26°47′N, 109°14′W, ca. 60 m, 14 Jan 1983, *T. Daniel et al. 2546* (holotype: CAS!; isotypes: ARIZ!, ASU!, ENCB!, MEXU!, MICH!, NY!, US!).

Phenology. January–March; August–October; fruiting: January–March; August–October.

Distribution and habitats. Northwestern Mexico (Sonora, Sinaloa); Sonoran plants occur in thornscrub and desert grasslands at elevations from 60 to 1100 m.

Illustration. *Brittonia* 47:409. 1995.

Daniel (1995c) provided a description of this species, which reaches its northern distributional extent in the grasslands of northeastern Sonora (Fig. 26).

Sonoran collections: Mpio. Navojoa, ca. 2 km N of Teachive, SW end of Cerro Terucuchi, 26°48′N, 109°14′W, *A. Reina et al. 96-581* (CAS, MEXU); ca. 1 mi SW of Mesa Masiaca, E side of Hwy. 15, 8.8 mi S of jct. with Hwy. 176 near KM 116 (S of Navojoa), *T. Van Devender & A. Sanders 92-1058* (ARIZ, CAS, MO, TEX); 1.3 km W of Hwy. 15 on Huatabampo Rd, ca. 22 km S of Navojoa, 26°49′N, 109°23′W, *T. Van Devender et al. 93-257* (ARIZ, ASU, CAS, DAV, MO, SD, TEX, UCR); 9.3 km E of Masiaca on road to Yocojigua, 26°45′N, 109°08′W, *T. Van Devender et al. 93-827* (ARIZ, CAS); region of the Río de Bavispe, Cañón de las Bellotas, *S. White 3590* (GH); region of the Río de Bavispe, Cañón del Agua Amarga, *S. White 3590* (ARIZ, US).

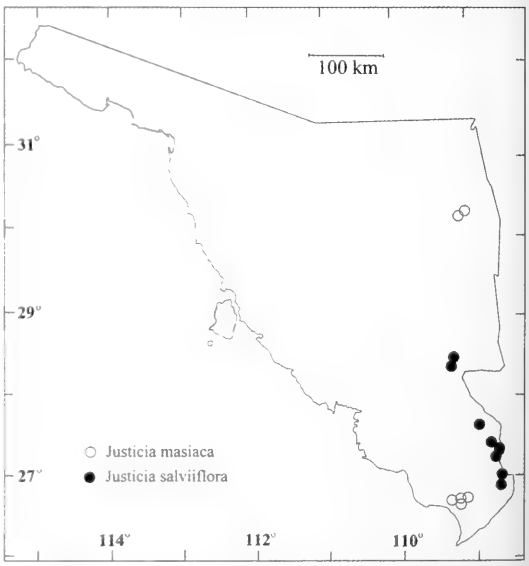


Figure 26. Sonoran distributions of *Justicia masiaca* and *J. salviiflora*.

Justicia phlebodes Leonard & Gentry, Brittonia 6:327. 1948. TYPE: MEXICO. Sinaloa: Sierra Tacuichamona, between Culiacán and Mazatlán and S of the Río San Lorenzo, near Africa, 17 Feb 1940, *H. Gentry 5652* (holotype: US; isotypes: DS!, GH!, MICH).

Perennial herbs to 1 m tall. Younger stems subterete to subquadrate, pubescent with flexuose to retrorse to retrorsely appressed eglandular trichomes 0.3–1 (–1.5) mm long, trichomes concen-

trated in or restricted to 2 lines or ± evenly disposed. Leaves petiolate, petioles to 30 mm long, blades ovate-elliptic to elliptic to subcircular, 29–122 mm long, 12-70 mm wide, 1.1–2.7 times longer than wide, acute to subacuminate at apex, (truncate-subattenuate to) attenuate at base, surfaces pubescent (trichomes sometimes restricted to major veins) with flexuose to antrorse eglandular trichomes to 1 mm long, margin entire to subsinuate, usually ciliate. Inflorescence of axillary (in axils of leaves or inflorescence bracts distally) or terminal dichasiate spikes (or panicles of spikes), rachises (of both panicles and spikes) evenly pubescent with erect eglandular (sometimes inconspicuous) and glandular trichomes 0.05–0.3 mm long (glandular pubescent); dichasia opposite (to alternate), sessile, 1 per axil, 1-flowered. Bracts (including those subtending spikes and dichasia) elliptic to obovate, 4–7 mm long, 1.2–3 mm wide, abaxial surface glandular pubescent. Bracteoles lance-linear to linear, 4.8–6.5 mm long, 0.5–0.7 mm wide, abaxial surface glandular pubescent. Flowers sessile. Calyx 4-lobed, (5–) 6.5–9 mm long, lobes linear, (4.5–) 5.2–7.5 mm long, equal to subequal in length, 0.4–0.7 mm wide, abaxially glandular pubescent. Corolla 19–28 mm long, pink-purple, externally glandular pubescent, tube cylindric (expanded slightly only near apex), 13-23 mm long, 0.9–1.2 mm in diameter near midpoint, upper lip 4–6 mm long, entire to 2-fid at apex, lobes to 0.6 mm long, lower lip 4–7 mm long, lobes 3–4.5 mm long, 2–3.5 mm wide. Stamens inserted near apex of corolla tube, 3.5–5 mm long, filaments glabrous, thecae pink-purplish, subparallel to parallel, superposed (gap 0.4–0.7 mm long), unequal in size, upper theca 1.3–1.5 mm long, glabrous, lacking a basal appendage, lower theca 1–1.2 mm long (including basal appendage), glabrous, with a basal appendage 0.2 mm long; pollen (Fig. 20) 2-aperturate, apertures flanked on each side by 2–2.5 rows of insulae (to peninsulae). Style pink-purplish, 16.5–22 mm long, pubescent (at least proximally) with eglandular (and sometimes a few glandular) trichomes, stigma 0.4–0.5 mm long, only 1 lobe evident. Capsule 7–8 mm long, externally glandular pubescent (or with some of the eglandular trichomes retrorse), stipe 2–2.5 mm long, head subellipsoid with a slight medial constriction. Seeds 4 per capsule, sublenticular, 1.5–1.7 mm long, 1–1.3 mm wide, surface and margin tuberculate.

Phenology. Flowering: March, October–November; fruiting: March, October–November.

Distribution and habitats. Northwestern Mexico (Chihuahua, Durango, Sinaloa, Sonora); Sonoran plants occur in canyons and along watercourses in tropical deciduous forests and oak-pine forests at elevations from 320 to 1250 m.

Illustration. Figure 27.

Local name. "Cordoncillo" (*Fishbein et al. 178*).

Justicia phlebodes is endemic to northwestern Mexico and reaches the northwestern extent of its distribution in southern Sonora (Fig. 28).

Sonoran collections: trail to Tepopa from El Chiribo, 27°19′N, 108°44′W, *M. Fishbein et al. 178* (ARIZ), *199* (ARIZ); Mpio. Alamos, upper Río Cuchujaqui, Arroyo Santa Bárbara, 27°06.5′N, 108°43′W, *P. Jenkins et al. 92-99* (ARIZ, CAS, MO); Rancho San Pedro, El Cajón along Río Cuchujaqui, *P. Martin s.n.* (ARIZ); Rancho San Pedro, 23 km E, 4 km N of Alamos, 27°03′N, 108°42′W, *P. Martin et al. s.n.* (ARIZ); canyon N of Los Aguaros on Arroyo Guajaráy, 27°38.5′N, 108°58′W, *T. Van Devender et al. 93-483* (ARIZ, CAS).

Justicia salviiflora H.B.K., Nov. Gen. Sp. 2:233. 1818. *Sarotheca salviiflora* (H.B.K.) Nees in A. de Candolle, Prodr. 11:382. 1847. TYPE: cultivated in a Mexican botanical garden (fide protologue) (holotype: P-Bonpl.!; isotype: P!).

Justicia paniculata Rose, Contr. U.S. Natl. Herb. 1:348. 1895, non Burm f. (1768) nec Forsk. (1775) nec Sessé & Moc. (1887). TYPE: MEXICO. Colima: vicinity of Colima, 9 Jan–6 Feb 1891, *E. Palmer 1143* (holotype: US!; isotypes: K!, US!).

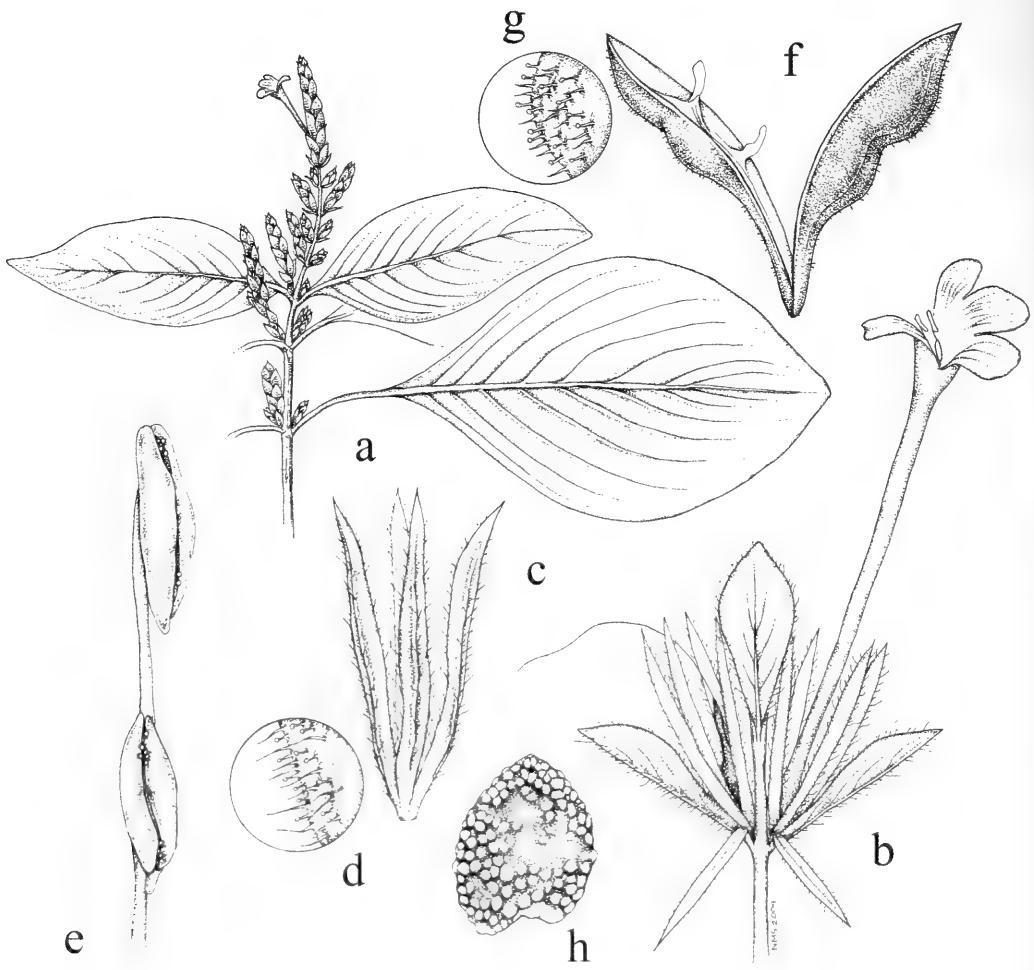


FIGURE 27. *Justicia phlebodes*. a. Habit (*Gentry 5652*), × 0.5. b. Inflorescence node with flower (*Van Devender et al. 93-483*), × 3.2. c. Calyx (*Van Devender et al. 93-483*), × 5.3. d. Trichomes on abaxial surface of calyx (*Van Devender et al. 93-483*), × 18. e. Distal portion of stamen with anther (*Van Devender et al. 93-483*), × 24. f. Capsule (*Jenkins et al. 92-99*), × 5.7. g. Trichomes on outer surface of capsule (*Jenkins et al. 92-99*), × 25. h. Seed (*Van Devender et al. 93-483*), × 17. Drawn by Nadia Strasser.

Phenology. Flowering: March–April; fruiting: March–April.

Distribution and habitats. Mexico (Chiapas, Chihuahua, Colima, Durango, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Sinaloa, Sonora); Sonoran plants occur along watercourses, on rocky slopes, and in disturbed areas in tropical deciduous forests and oak woodlands at elevations from 310 to 580 m.

Illustrations. Figure 9; *The Botany of the Voyage of H.M.S.* Herald, t. 67. 1856; *Flora of Chiapas* 4:78. 1995.

Daniel (1995a) provided a detailed description of this species, which reaches the northern and western extents of its distribution in southeastern Sonora (Fig. 26). Sonoran plants are perennial herbs or shrubs that sometimes appear somewhat vinelike with secondary rooting at the nodes. Corollas are whitish with a green upper lip and purple striped ridges on the lower lip.

Sonoran collections: Arroyo Guajaráy, between Los Aguaros & Cajón del Ardilla, 27°39′N, 108°58′W, *R. Felger et al. 94-58A* (ARIZ); Río Mayo Region, Agua Salado, 15 mi NE of Los Tanques, 27°15′N, 108°46′W, *M. Fishbein et al. 85* (ARIZ); Río Mayo Region, Arroyo Guajaráy, just N of Los Aguaros, 27°38′N, 108°58′W, *M. Fishbein et al. 1565* (ARIZ, CAS); Río Mayo Region, Tepopa, *H. Gentry 1433* (A, ARIZ, F, MEXU, MO, UC, WIS), *1435* (MEXU); Río Mayo Region, Arroyo Gochico, *H. Gentry 3624* (ARIZ, F, GH, MEXU, MO, UC, US); Mpio. Alamos, Upper Río Cuchujaqui, cajón of the Cuchujaqui, 27°02′N, 108°42′W, *P. Jenkins 89-438* (ARIZ, CAS); Mpio. Yécora, Arroyo del Pilladito, near Tepoca, 28°26′N, 109°15′W, *A. Reina G. & T. Van Devender 97-337* (ARIZ, CAS, MEXU, TEX); Mpio. Alamos, 9.5 km N of Güirocoba along road to Choquincahui (El Cobre), ca. 26°58′N, 108°41′W, *V. Steinmann et al. 616* (ARIZ, MEXU); 1 km W of Son. 12 (Tepoca-Cd. Obregón Hwy.) on road to La Quema, 28°22′N, 109°16′W, *W. Trauba 216-98* (CAS).

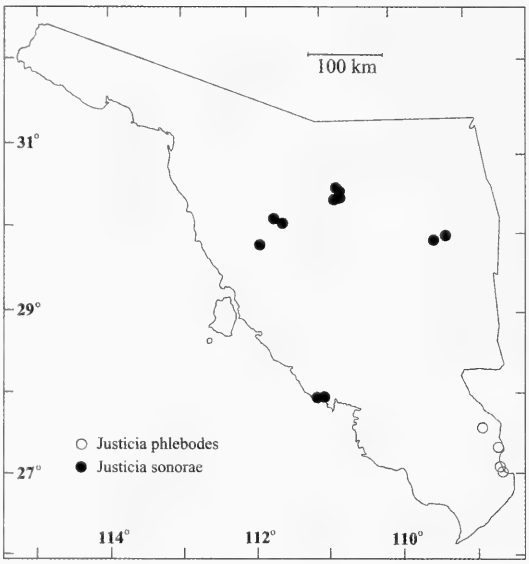


FIGURE 28. Sonoran distributions of *Justicia phlebodes* and *J. sonorae*.

Justicia sonorae Wassh., Phytologia 49:65. 1981. TYPE: MEXICO. Sonora: 17.2 mi SSE of Magdalena, palm canyon in Cerro Cinta de Plata (= Sierra Babiso), 13 Feb 1977, *T. Van Devender s.n.* (holotype: US!; isotypes: ARIZ!, GH!, UC!).

Ascending to erect perennial herbs to 4.5 dm (–1 m) tall. Young stems subterete to quadrate-sulcate to hexagonal, glabrous or evenly to bifariously to unifariously pubescent with flexuose to retrorse (to retrorsely appressed) eglandular trichomes 0.2–1 mm long, sometimes also with scattered glandular trichomes (usually restricted to distal few internodes) 0.05–0.3 mm long. Leaves (plants sometimes leafless during anthesis) petiolate, petioles to 5 (–7) mm long, blades lance-ovate to ovate (to cordate), 7–55 mm long, 3–22 mm wide, 1.3–2.8 times longer than wide, acute to acuminate at apex, truncate to rounded to acute at base, surfaces pubescent with mostly erect to flexuose eglandular trichomes to 1 mm long. Inflorescence of axillary or terminal dichasiate spikes to 15 cm long, these sometimes basally branched (and thus becoming a panicle of spikes), spikes (when several) collectively forming a terminal ± leafy panicle, spike rachises evenly pubescent with erect to flexuose to retrorse eglandular and glandular trichomes 0.05–0.3 mm long (glandular pubescent); dichasia (alternate to) opposite (sometimes opposite a fertile branch), sessile, 1 per axil, 1-flowered. Bracts opposite, triangular-subulate to lance-subulate, 1–4.8 mm long, 0.8–1.5 mm wide, abaxial surface glandular pubescent (or the glandular trichomes sometimes absent). Bracteoles lance-subulate, 1.2–3.2 mm long, 0.3–0.8 mm wide, abaxial surface pubescent like bracts. Flowers sessile. Calyx 4–5-lobed, 3–6 mm long, 4 lobes equal, lanceolate, 2.5–5 mm long, 0.4–0.7 mm wide, abaxially glandular pubescent, posterior 5th lobe (if present) filiform, 0.3–2 mm long. Corolla pinkish purple with white markings on lower lip, 23–37 mm long, externally glandular pubescent, tube funnelform (gradually expanded distally), 18–25 mm long, 1.8–2.7 mm in diameter near midpoint, upper lip 6.5–12 mm long, entire, lower lip 8–17 mm long, lobes elliptic, 4–9 mm long, 3–6 mm wide. Stamens inserted near apex of corolla tube, 7–11 mm long, filaments glabrous, thecae 1.2–2.2 mm long, subequal, parallel to subparallel, subequally inserted, lacking

basal appendages, glabrous (or sometimes the upper theca dorsally pubescent with eglandular trichomes to 0.1 mm long); pollen (Fig. 20) 2-aperturate, apertures flanked on each side by 2 rows of insulae. Style 19–34 mm long, proximally pubescent with eglandular trichomes, stigma 0.3–0.4 mm long, 1 lobe 0.3–0.4 mm long, other lobe not evident or up to 0.2 mm long. Capsule 10–13.5 mm long, externally glandular pubescent, stipe 3–5.5 mm long, head ellipsoid with a slight medial constriction. Seeds 4, 1.8–2.5 mm long, 1.4–2.3 mm wide, surfaces and margin bubbly tuberculate. ($n = 11$).

Phenology. Flowering: September–April; fruiting: November–April.

Distribution and habitats. Southwestern United States (Arizona) and northwestern Mexico (Sinaloa, Sonora); Sonoran plants occur along watercourses and on slopes in Sonoran desertscrub (Central Gulf Coast, Plains of Sonora), palm oases, and thornscrub at elevations from near sea level to 1230 m.

Illustration. Figure 6; *Phytologia* 49:67. 1981.

Justicia sonorae is known from relatively few collections, but appears to have a broad distribution in Sonora (Fig. 28). The species shares several morphological features (e.g., inflorescence form and pubescence, corolla shape and pubescence, pollen, capsule shape and pubescence) with *J. hians* (Brandegee) Brandegee of Baja California Sur. These species can be distinguished by the following couplet:

1. Single-flowered dichasia alternate along rachis; calyx with 5 conspicuous lobes (posterior lobe only slightly shorter than other four lobes); corolla orange red, upper lip 12.5–16.5 mm long, 2-lobed at apex, lobes of lower lip 1.8–3.5 mm wide; young stems evenly and densely pubescent with trichomes 0.05–0.1 (–0.2) mm long; Baja California Sur. . . . . *J. hians*
1. Single-flowered dichasia mostly opposite along rachis; calyx with 4 conspicuous lobes (posterior or fifth lobe, if present, inconspicuous and less than 1/2 as long as other 4 lobes); corolla pinkish purple, upper lip 6.5–11 mm long, entire at apex, lobes of lower lip 4–8 mm wide; young stems glabrous or evenly to bifariously to unifariously pubescent with trichomes 0.2–1 mm long; Arizona, Sonora, and Sinaloa. . . . . *J. sonorae*

Justicia sonorae is also similar to the Oaxacan species *J. santelisiana* Acosta & T.F. Daniel. The latter species differs by the eglandular (only) trichomes on the external surface of the corollas and capsules, smaller (2–3.7 mm long and 1.8–3.3 mm wide) lobes of the lower lip of the corolla, longer (12–16 mm) stamens, longer (13.5–15 mm) capsules, and longer (2.7–3 mm) seeds.

Other plants that resemble *J. sonorae* are represented by two collections from the vicinity of Bahía Topolobampo in northwestern Sinaloa (e.g., *Reina G. et al. 98-2070* at ARIZ, ASU, CAS, MEXU, NY; *Gentry 14312* at US). These plants have red corollas and few glands on the inflorescence rachis, but appear otherwise indistinguishable from pink-purple-flowered individuals of *J. sonorae*, in which species they are tentatively included as a red-flowered form. *Rose et al. 13291* (US) was also collected from the vicinity of Topolobampo. Color of the corolla is neither noted nor preserved on this specimen, but it more closely resembles the majority of collections of *J. sonorae* by having a conspicuously glandular rachis.

Sonoran collections: 0.8 mi W of abandoned mine in pass between Cerro San Luis and Sierra Santa Rosa, 30.1°N, 111.6°W, *J. Bowers & R. Turner 2196* (ARIZ); Palm Canyon, 17 mi SE of Magdalena in Cerro Cinta de Plata (Sierra Babiso), *M. Fay 714* (ARIZ); Cerro Tetas de Cabra, Bahía San Carlos, *R. Felger 85-366* (ARIZ, MEXU, TEX); Rancho San Jorge, W of Hermosillo, ca. 29°44′N, 111°51′W, *R. Felger & A. Russell 6909* (ARIZ); Cañón Nacapules, ca. 4 km N of Bahía San Carlos, *R. Felger & B. Straub 85-1301* (ARIZ); Bahía San Carlos, *H. Gentry 11341* (ARIZ, LL); 2.6 mi E of bridge at Huásabas, *L. Landrum et al. 5435* (CAS, GH, MO, NY); Algadones Bay area, 4 mi W of San Carlos Bay, *P. Martin s.n.* (ARIZ); Palm

Canyon, 17 mi SE of Magdalena on road to Cucurpe, Sierra Baviso, *N. McCarten & R. Bittman 2693* (ARIZ); 7.7 mi S of Cucurpe, *L. McGill et al. 6534* (ENCB); Palm Canyon, 15.5 mi SE of Mex. 15 at Magdalena toward Cucurpe, *F. Reichenbacher 916* (ARIZ, CAS); N end of Sierra Santa Rosa, 22 mi SSW of Trincheras, ca. 30°06′N, 111°39′W, *A. Sanders et al. 3600* (CAS, UC); 10 mi N of San Carlos, *D. Shaw 30* (MO); Palm Canyon, 17 mi SE of Magdalena, Cerro Cinta de Plata (Sierra Babiso), *D. Steadman & K. Schmidt s.n.* (ARIZ); near Palm Canyon, 17 mi E of Magdalena, *R. Thompson & O. Davis 82-44* (ARIZ); Mpio. Santa Ana, Rancho El Otate, Arroyo Los Otates, 30°18′N, 110°53′W, *T. Van Devender & A. Reina G. 98-434* (ARIZ, CAS, MEXU, NY, TEX); 20.4 mi SE of Magdalena on Cucurpe road, *T. Van Devender et al. s.n.* (ARIZ); KM 101 on Hermosillo-Moctezuma road, 38.6 mi E of Moctezuma, 29°28′N, 110°15′W, *A. Whittemore et al. 83-099* (TEX).

Justicia spicigera Schltdl., Linnaea 7:395. 1832. *Jacobinia spicigera* (Schltdt.) L.H. Bailey, Standard Cyclopedia of Horticulture, 1715. 1915. TYPE: MEXICO. Veracruz: Jalapa, May 1829, *A. Schiede s.n.* (syntype: B, destroyed; isosyntypes: BR!, GH; probable isosyntypes: E!, P!); Veracruz: cultivated at Hacienda de la Laguna, Jul 1829, *A. Schiede s.n.* (syntypes: B, destroyed, P!; isosyntype: BM!).

See Daniel (1995a) for a complete list of synonyms.

Phenology. Flowering: March, July; fruiting: unknown.

Distribution and habitats. Mexico (Baja California Sur, Chiapas, Guerrero, Hidalgo, Jalisco, México, Michoacán, Nayarit, Oaxaca, Puebla, Querétaro, Veracruz, Yucatán), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica; Sonoran plants are cultivated (and possibly persisting after or escaping from cultivation) at elevations from 330 to 700 m.

Illustrations. *Fieldiana, Botany* 24(10):401. 1974; *Flora of Baja California*, 193. 1980; *Flora of the Bahama Archipelago*, 1352. 1982; *Mexican Roadside Flora*, 25. 1987.

Local name. "Niple" (*Joyal 2059*).

Use. Leaves are boiled with cinnamon to yield a clear, red tea that is taken for stomach pain (*Joyal 2059*).

Daniel (1995a) and Daniel and Acosta (2003) provided descriptions of this species. *Rose et al. 13020* was noted to have been "apparently" cultivated and *Joyal 2059* was noted to be planted in a "house garden." *Justicia spicigera* is widely cultivated throughout Mexico such that the actual native distributional range of the species is not known with certainty. It is undoubtedly considerably smaller than suggested by the states listed above.

Sonoran collections: Mpio. Onavas, Rancho El Palmar, 20 km E of Onavas, 28°29–30′N, 109°23′W, *E. Joyal 2059* (CAS); vicinity of Alamos, *J. Rose et al. 13020* (US).

Odontonema Nees

Odontonema Nees, Linnaea 16:300. 1842, nom. cons. TYPE: garden specimen without date or collector (GZU), type cons.

Thyrsacanthus Nees in Martius, Fl. Bras. 9:97. 1847, nomen superfl. (= *Odontonema*).

Diateinacanthus Lindau, Bull. Herb. Boissier, ser. 2, 5:369. 1905. TYPE: *Diateinacanthus hondurensis* Lindau (≡ *Odontonema hondurense* (Lindau) D.N. Gibson).

Erect perennial herbs or shrubs (sometimes clambering) with cystoliths. Leaves opposite. Inflorescence of mostly terminal and sometimes basally branched dichasiate spikes, racemes, or thyrses; dichasia alternate to opposite to whorled, 1-many (i.e., 18 or more)-flowered, variously contracted or expanded, sessile or pedunculate, subtended by a bract. Flowers homostylous or heterostylous, usually pedicellate, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes equal in length. Corolla infundibular, white, yellow, purple, pink, or red, tube usually expand-

ed distally into a prominent throat, limb subactinomorphic to 2-labiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes imbricate in bud. Stamens 2, thrum stamens exserted from mouth of corolla, pin stamens usually included in corolla tube, anthers 2-thecous, thecae equal in size, parallel, equally inserted on filament, lacking basal appendages, dehiscing toward lower lip (i.e., flower nototribal); pollen oblate spheroidal to spherical to euprolate, 3(–4)-colporate, 6(–8)-pseudocolpate, pseudocolpi 2 per mesocolpium, exine foveolate to rugulate to reticulate to bireticulate; staminodes 2. Thrum style included in corolla tube, pin style exserted from mouth of corolla, stigma ± funnelform or 2-lobed, lobes equal or unequal in length. Capsule stipitate, head obovoid to subellipsoid (often with a medial constriction), retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule. Seeds 4, homomorphic, lenticular, lacking trichomes. ($x = 21$).

This genus of 29 species is restricted to the New World tropics and subtropics with eight species in Mexico (Daniel 1995d). Species with tubular, red corollas (like ours) are visited, and appear to be well adapted for pollination, by hummingbirds (see Daniel 1995d).

Odontonema cuspidatum (Nees) Kuntze, Revis. Gen. Pl. 2:494. 1891. *Thyrsacanthus cuspidatus* Nees in A. de Candolle, Prodr. 11:323. 1847. TYPE: MEXICO. Oaxaca: Sierra S. Pedro Nolasco, Talea, etc., 1843–1844, *C. Jürgensen 985* (lectotype designated by Daniel, 1995a: K!; isolectotype: BM!).

Phenology. Flowering: November; fruiting: unknown.

Distribution and habitats. Mexico (Chiapas, Guanajuato, Hidalgo, Morelos, Oaxaca, Querétaro, San Luis Potosí, Tabasco, Veracruz), Honduras, West Indies; Sonoran plants are cultivated and likely escaped (see below).

Illustration. *Contributions from the University of Michigan Herbarium* 20:157. 1995.

Daniel (1995a, 1995d) provided descriptions of *Odontonema cuspidatum*. This species of shrubs with red flowers is often cultivated for ornament. The sole Sonoran specimen from a natural habitat is rather fragmentary, but it does permit a tentative species identification. On the basis of the color of the corolla noted on the label (red) and the pubescence of the inflorescence rachis (mostly erect and evenly disposed eglandular trichomes 0.05–0.2 mm long) this collection resembles *O. cuspidatum*, a species of eastern and southern Mexico (Daniel 1995d). It differs from that species, and resembles *O. glaberrimum* (M.E. Jones) V.M. Baum, by its mostly sessile to subsessile dichasia (although some dichasia are borne on peduncles 0.5–1 mm long). *Odontonema glaberrimum* is known from northern Sinaloa, but differs from *Jenkins & Yetman 91-115* by its rachises that vary from glabrous to pubescent with flexuose to antrorse eglandular trichomes 0.05-0.5 mm long. The number of apertures on pollen grains can be used to distinguish *O. cuspidatum* (pollen 4-aperturate; Fig. 18) from other Mexican species of the genus (all of which have 3-aperturate pollen; see palynological information in Daniel 1995d). Examination of pollen from *Jenkins & Yetman 91-115* (Fig. 18) reveals somewhat aberrant grains with four or more apertures. I suspect that *Jenkins & Yetman 91-115* represents an escaped occurrence of *O. cuspidatum* (with somewhat unusual sessile to subsessile dichasia and slightly deformed pollen), which is known to be cultivated for ornament in Sonora. Although *Jenkins & Yetman 91-115* was not collected near human dwellings, Jenkins (pers. comm.) indicates that there is a small settlement upstream from which propagules of this species could have washed downstream.

Sonoran collections: cultivated grounds of La Ciudadela just off Plaza de Armas in Alamos, ca. lat. 27°01′N, 108°56′W, *T. Daniel 9774* (CAS); near jct. of Arroyo Santa Bárbara with Arroyo Verde, 27°05′N, 108°43′W, *P. Jenkins & D. Yetman 91-115* (ARIZ, CAS).

Pseuderanthemum Radlk.

Pseuderanthemum Radlk., Sitzungsber. Math.-Phys. Kl. Akad. Wiss. München 13:282. 1883. LECTOTYPE (Leonard, Contr. U.S. Natl. Herb. 31(2):292. 1953; see J. Adelaide Bot. Gard. 9:141. 1986): *Pseuderanthemum alatum* (Nees) Radlk. (≡ *Eranthemum alatum* Nees).

Siphoneranthemum (Oerst.) Kuntze, Revis. Gen. Pl. 2:494. 1891. *Eranthemum* L. subg. *Siphoneranthemum* Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:166. 1855. TYPE: *Siphoneranthemum fasciculatum* (Oerst.) Kuntze (≡ *Eranthemum fasciculatum* Oerst.).

Buceragenia Greenm., Proc. Amer. Acad. Arts 32:303. 1897. TYPE: *Buceragenia minutiflora* Greenm.

Decumbent to erect herbs or shrubs with cystoliths. Leaves opposite. Inflorescence of dichasia in leaf axils or of axillary or terminal dichasiate spikes, racemes, thyrses, or panicles; dichasia opposite or alternate, 1–many-flowered, sessile or pedunculate, subtended by a leaf or bract. Flowers chasmogamous and/or cleistogamous, homostylous or heterostylous, sessile or pedicellate, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes homomorphic. Corolla white, pink, blue, purplish, or red, the lower lip sometimes with colored markings, ± salverform (i.e., with a prominent slender tube and a rotate limb), tube cylindric, sometimes ± expanded distally into a short throat, limb subactinomorphic to bilabiate, upper lip 2-lobed, lower lip 3-lobed, corolla lobes imbricate in bud, corollas of cleistogamous flowers remaining budlike. Stamens 2, included in corolla tube or exserted from mouth of corolla, anthers 2-thecous, thecae equal to subequal in size (or in cleistogamous flowers becoming unequal or with 1 theca suppressed), parallel, subequally inserted, lacking basal appendages, dehiscing introrsely toward lateral lobes of corolla (i.e., flower pleurotribal); pollen (Fig. 18) oblate spheroidal to euprolate, 3-colporate (sometimes syncolpate), 6-pseudocolpate, pseudocolpi 2 per mesocolpium, the 2 sometimes fused near poles into pseudocolpal ellipses, exine (rugulate to) reticulate; staminodes 0 or 2. Style included in corolla throat or exserted from mouth of corolla, stigma 2-lobed, lobes equal. Capsule stipitate, head ellipsoid with a medial constriction, retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule. Seeds 4, homomorphic, plano-convex to lenticular, lacking trichomes. ($x = 21$)

This genus of 40-60 species occurring in the tropics worldwide is in need of considerable study. Its relationships to *Odontonema, Chileranthemum, Pulchranthus* and *Oplonia* are especially problematic in the New World. Cleistogamy and heterostyly are both present in *Pseuderanthemum* and have added to taxonomic confusion in the genus. Species previously treated in *Buceragenia* represent plants of *Pseuderanthemum* with cleistogamous flowers (Daniel 1995b). There are 10–15 species in Mexico. Sonoran plants of *Pseuderanthemum* are indicative of the problems involved in delimiting and identifying Mexican species of the genus.

Pseuderanthemum praecox (Benth.) Leonard, J. Wash. Acad. Sci. 31:99. 1941. *Eranthemum praecox* Benth., Pl. Hartweg. 291. 1848-1849. *Siphoneranthemum praecox* (Benth.) Kuntze, Revis. Gen. Pl. 2:497. 1891. TYPE: MEXICO. Guanajuato: Santa Rosa near Guanajuato, 1837, *T. Hartweg 1614* (holotype: K!).

Perennial herbs to 5.5 dm tall. Young stems subquadrate to ± compressed, sometimes ± multistriate, glabrous or ± evenly (to ± bifariously) pubescent with retrorse to flexuose eglandular trichomes 0.05–0.2 (–0.3) mm long. Leaves generally absent when chasmogamous flowers present in spring, present along with cleistogamous flowers in late summer, membranaceous, sessile to

petiolate, petioles to 3 (–12) mm long, blades either linear to lanceolate, 66–200 mm long, 4–15 mm wide, 7.7–23 times longer than wide, acute to attenuate at base, attenuate at apex, or blades narrowly elliptic to elliptic to lance-ovate to ovate to obovate, 37–100 mm long, (7–) 16–37 mm wide, mostly 1.7–4.7 (–5.7) times longer than wide, acute to attenuate at base, attenuate to acute to rounded at apex, surfaces of all blades glabrous or pubescent (especially along veins) with flexuose to retrorse to retrorsely appressed eglandular trichomes 0.05–0.2 mm long, margin flat, entire to subsinuate. Inflorescence of ± congested dichasia in axils of leaves and sometimes also in axils of bracts distally, the latter forming a terminal spikelike raceme or thyrse, rachis (if present) glabrous or pubescent like young stems; dichasia opposite or alternate, sessile to pedunculate, 1–4-flowered, peduncles to 3 (–50) mm long. Bracts (if present) subulate to linear, 2–14 (–43) mm long, 1–1.2 (–2) mm wide, abaxial surface glabrous or pubescent with flexuose to antrorse to retrorse eglandular trichomes 0.05–0.1 mm long. Bracteoles and secondary bracteoles usually triangular to subulate, 1.2–5 mm long, 0.7–1.2 mm wide (sometimes foliose, lanceolate to linear to elliptic to ovate, to 36 mm long and 17 mm wide), abaxial surface glabrous or pubescent with flexuose to antrorse to retrorse eglandular trichomes 0.05–0.1 mm long. Flowers subsessile to pedicellate, pedicels 0.05–3.5 (–5) mm long. Calyx 3.5–7 (–9.3 in fruit) mm long, lobes subulate, 2.5–5.5 (–8.5) mm long, 2.5–4.5 (–5.5) times longer than tube, abaxially nearly glabrous or pubescent like bracteoles (occasionally with a few sessile or stipitate inconspicuous glands to 0.1 mm long as well), or pubescent with erect to flexuose eglandular trichomes and conspicuous glandular trichomes 0.05–0.2 mm long. Corolla of chasmogamous flowers salverform, pink to light purplish with white area on lower lip near mouth, 20–35 mm long, externally sparsely pubescent near apex of lobes with flexuose eglandular trichomes, otherwise glabrous, tube subcylindric, 19–21 mm long, 0.9–1.1 mm in diameter near midpoint, expanded slightly above middle into a ± inconspicuous throat, limb subactinomorphic (lobes similar, elliptic to ovate-elliptic), 17–24 mm in diameter, upper lip 7–13 mm long, lobes 7–13 mm long, 3.5–5.7 mm wide, lower lip 10–14 mm long, lobes 8.7–13 mm long, (4–) 4.7–7 mm wide; corolla of cleistogamous flowers budlike, white with purple at apex, 2–2.5 mm long, apically pubescent with flexuose eglandular trichomes 0.05–0.1 mm long. Stamens of chasmogamous flowers included, 3.5–4 mm long, thecae 2–2.5 mm long; staminodes up to 0.6 mm long. Style of chasmogamous flowers included (or with stigma barely exserted from mouth), 17–18 mm long, glabrous, stigma lobes 0.2–0.3 mm long, equal; style of cleistogamous flowers 1–1.2 mm long, glabrous, curved to recurved apically, stigma subequally 2-lobed, 0.2 mm long. Capsule 13–18 mm long, glabrous, stipe 5–7 mm long, head 8–11 mm long. Seeds planoconvex to concavo-convex, 2.9–4.5 mm long, 2.5–3.6 mm wide, surfaces irregularly reticulate-ridged, ridges sometimes reduced to knoblike projections on mature seeds.

Phenology. Flowering March–May (chasmogamous flowers), August–September (cleistogamous flowers); fruiting: March–May, August–October.

Distribution and habitats. Mexico (Chiapas, Distrito Federal, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Oaxaca, Puebla, Querétaro, Sinaloa, Sonora, Tamaulipas, Zacatecas), Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica; in Sonora plants occur in along watercourses and on rocky slopes in oak woodlands, oak forests, oak-pine woodlands, and oak-pine forests at elevations from 1100–1580 m.

Illustrations. Figures 15, 29; *Flora de Valle de México*, fig. 297B. 1979; *Flora del Valle de Tehuacán-Cuicatlán* 23:66. 1999; *Flora del Bajío* 117:118. 2003.

Descriptions of this species from other regions of Mexico have been provided by Daniel (1995a, 1999a) and Daniel and Acosta (2003). A description based exclusively on Sonoran plants is presented here because they exhibit morphological variation not observed in these other regions. All Sonoran plants of *Pseuderanthemum* are interpreted as pertaining to a single species, *P. prae-*

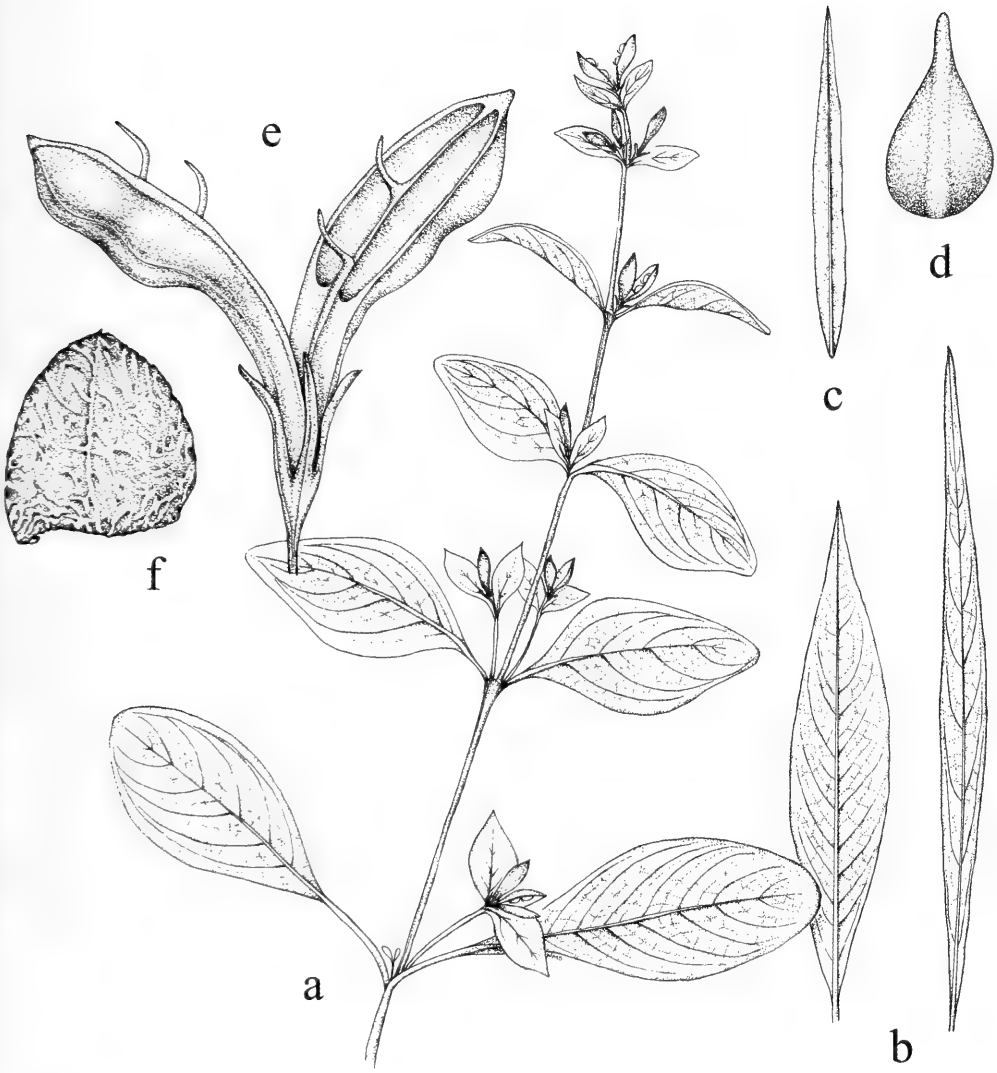


FIGURE 29. *Pseuderanthemum praecox*. a. Habit (*Reina G. & Van Devender 99-529*), × 0.58. b. Leaves, × 0.58: narrow leaf on right (*Reina G. & Van Devender 98-1700*), wider leaf on left (*Reina G.& Van Devender 99-527*). c. Bracteole from lower node (*Reina G. & Van Devender 99-666*), × 7.5. d. Bracteole from upper node (*Reina G. & Van Devender 99-666*), × 10.4. e. Capsule (*Reina G. & Van Devender 99-666*), × 4.1. f. Seed (*Reina G. & Van Devender 99-666*), × 8.1. Drawn by Nadia Strasser.

cox. It is evident from the above description that *P. praecox* in Sonora exhibits considerable morphological diversity. This variation appears to be attributable to seasonality, cleistogamy, and morphological plasticity.

Generally leafless plants with chasmogamous flowers have been collected in the spring (March–May) whereas leafy plants with only cleistogamous flowers have been collected only during the late summer (August–September). Based on the many collections of plants from riparian communities in a region of oak-pine woodland and forest (between Yécora and the Chihuahua border) and the summary of climatic data for the region by Van Devender et al. (2003), the life cycle

of *P. praecox* there can by hypothesized as follows: new, leafy shoots appear from the underground caudex in the late summer in response to the summer (June–October) rains; these shoots bear cleistogamous flowers that self-pollinate and yield fruits that mature prior to winter; the leaves are deciduous and fall sometime during the winter months when extended periods of freezing temperatures are common; following the winter rains (November–February) and the end of freezing temperatures in the spring, the old (and now leafless) shoots bear new growth from the axillary buds that bears chasmogamous flowers; these flowers are potentially available for cross-pollination, but likely self-pollinate as the corolla falls from the flower if pollination has not been otherwise effected; fruits mature prior to the death (and collapse) of these shoots during the dry period of late spring and summer. The two seasonal phases of Sonoran plants of *P. praecox* can be distinguished by the following couplet:

1. Chasmogamous flowers present, corollas salverform 20–35 mm long; leaves mostly or entirely absent; calyx pubescent with eglandular and conspicuous glandular trichomes. . spring phase
1. Chasmogamous flowers absent, only cleistogamous flowers present, corollas budlike, 2–2.5 mm long; leaves present; calyx nearly glabrous or pubescent with eglandular (and often inconspicuous glandular) trichomes . . . . . late summer phase

I have not observed the late summer phase in other portions of the range of *P. praecox* in Mexico (for example, 41 of the 42 Mexican (non-Sonoran) specimens of *P. praecox* at MEXU are entirely or nearly leafless, have chasmogamous flowers, and were collected between December and June-but mostly in March and April; the other collection was leafless, but lacked corollas), but it may be represented by one or more species previously treated under *Buceragenia* (see Daniel 1995b).

Sonoran plants of *Pseuderanthemum praecox* are unusual in having two foliar forms (although with some intermediacy between them) and two pubescence forms, all growing together. Most collections have the leaf blades either very narrow, linear, and 7.7–23 times longer than wide (e.g., *Gentry et al. 19402*; *Reina G. & Van Devender 98-1700*, *99-666*, *2000-629*; *Reina G. et al. 2000-379*) or wider, elliptic to obovate, and 1.3–5.7 times longer than wide (e.g., *Reina G. & Van Devender 98-1863*, *99-529*, *2000-623*; *Reina G. et al. 2000-380*; *Van Devender & Reina G. 98-1832*). Plants with both types of leaf blades or with the blades somewhat intermediate between the two forms occur in a population west of Maycoba. For example, *Reina G. & Van Devender 99-525* has both linear (22.5 times longer than wide) and lance-ovate (4.9 times longer than wide) leaf blades. *Reina G. & Van Devender 99-527* has leaves varying from 3.3–6.1 times longer than wide. It is not known whether plants with linear leaves represent a riverine morphological form, with the broader leaved plants occurring on somewhat drier sites. Plants with narrow, linear leaves appear to have been first collected by Howard Gentry in October 1961 from the Sierra Tecurahui in southeastern Sonora (east of Alamos, near the Chihuahua border) at an elevation between 1200 and 1360 meters. In their explorations in the Municipio de Yécora, Ana Lilia Reina G. and Tom Van Devender located similar plants in a tributary of Arroyo Pilares (west of Maycoba) at 1300 meters elevation, and recollected it there many times in efforts to document the foliar variation and flower type. Some plants from both of these populations have stems, leaves, and bracteoles glabrous (e.g., *Gentry et al. 19402* at ARIZ, *Reina G. et al. 99-525* at CAS), whereas other plants at these sites have these organs conspicuously pubescent (e.g., *Gentry et al. 19420* at US, *Reina G. et al. 99-525* at CAS).

The structure of the inflorescence is somewhat variable in *P. praecox*. In most individuals, the reduced dichasia form a dense cluster of flowers in the axils of the leaves. Sometimes the leaves are replaced by bracts distally, resulting in a terminal spikelike raceme to thyrse. The transition

from leaves to bracts is either abrupt or gradual. On some individuals, especially at the proximal nodes of plants with the broader leaf blades, dichasia are borne on elongate peduncles (to 50 mm long) and bear foliose bracteoles. It is sometimes difficult to interpret whether such lateral growth consists of long-pedunculate dichasia (that sometimes continue to elongate sympodially) or lateral branches bearing lateral dichasia. Both appear to be present.

Pseuderanthemum praecox reaches the northwestern extent of its range in southeastern Sonora (Fig. 30), from the vicinity of Yécora southward to the vicinity of Alamos. It undoubtedly occurs in nearby regions of Chihuahua, but it has not yet been collected in that state. The entirety of variation described above for this species in Sonora has been documented at only a single site (i.e., 24.7 km W of Maycoba). The species is also somewhat difficult to circumscribe in other portions of its range. I have taken various approaches to treating *Pseuderanthemum praecox* and its relatives (e.g., *P. fasciculatum* (Oerst.) Leonard and *P. hispidulum* (Nees) Radlk.) in Chiapas (Daniel 1995a), south-central Mexico (Daniel and Acosta 2003), El Salvador (Daniel 2001), and Honduras (Daniel 2004a); none of them seems very satisfactory.

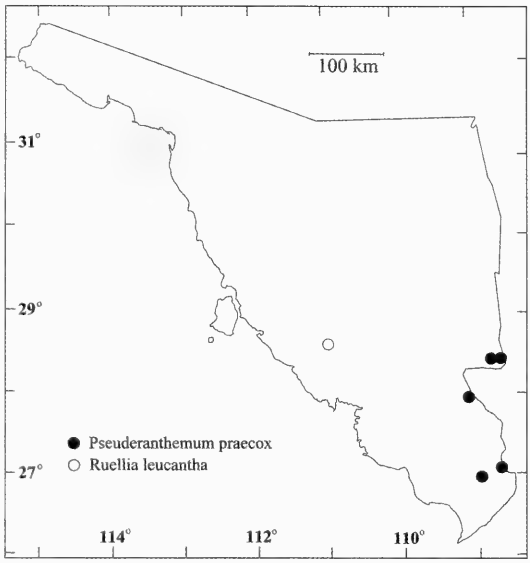


FIGURE 30. Sonoran distributions of *Pseuderanthemum praecox* and *Ruellia leucantha*.

SONORAN COLLECTIONS: Mpio. Yécora, Ciénega de Camilo, ca. 14 km E of Maycoba near Hwy. 16, ca. 28°26′N, 108°34′W, *T. Daniel et al. 8617* (CAS, K, MEXU); Rcho. Agrimincor, Río Mayo, *H. Gentry 3041* (ARIZ); Sierra Tecurahui, *H. Gentry et al. 19420* (ARIZ, US); Mpio. Alamos, Santa Bárbara, 27°07′N, 108°43′W, *P. Martin s.n.* (ARIZ); Mpio. Yécora, tributary of Arroyo Los Pilares near bridge, 24.7 km W of Maycoba on Mex. 16, 28°24′N, 108°48′W, *A. Reina G. & T. Van Devender 98-1700* (ARIZ, CAS), *98-1863* (CAS), *99-525* (ARIZ, CAS), *99-527* (CAS), *99-529* (CAS), *99-666* (CAS), *2000-623* (CAS), *2000-629* (CAS), *A. Reina G. et al. 2000-379* (CAS), *2000-380* (CAS); Mpio. Yécora, Arroyo Los Pilares, 21 km E of Yécora, 28°24′N, 108°47′W, *A. Reina G. et al. 96-59* (ARIZ, MEXU); Mpio. Alamos, Sierra de Alamos, ca. 4 km SW of Alamos at La Huerta, ca. 26°59′N, 108°58′W, *V. Steinmann 94-35* (ARIZ, CAS); Mpio. Yécora, Río Maycoba at Mex. 16 (20.5 km W of Maycoba, 28.6 km E of Yécora), 28°22.5′N, 108°45′W, *T. Van Devender & A. Reina G. 95-458* (ARIZ); Mpio. Yécora, Ciénega de Camilo, 6.3 km E of El Kípor, 11.2 km W of Chihuahua border, 28°25.5′N, 108°34′W, *T. Van Devender & A. Reina G. 97-402* (ARIZ, CAS), *98-1832* (CAS).

Ruellia L.

Ruellia L., Sp. Pl. 634. 1753. LECTOTYPE (Britton and Brown, Ill. Fl. N. U.S., ed. 2, 3:241. 1913): *Ruellia tuberosa* L.

Dipteracanthus Nees in Wallich, Pl. Asiat. Rar. 3:75, 81. 1832. LECTOTYPE (Bremekamp and Nannenga Bremekamp, Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk., Tweede Sect. 45(1): 15. 1948): *Dipteracanthus prostratus* (Poiret) Nees (≡ *Ruellia prostrata* Poiret).

Aphragmia Nees in Lindley, Intr. Nat. Syst. Bot., ed. 2, 444. 1836. TYPE: *Aphragmia haenkei* Nees (≡ *Ruellia inundata* H.B.K.).

Decumbent to erect subcaulescent to caulescent perennial herbs, shrubs, or (rarely) trees with

cystoliths, vegetative and floral surfaces sometimes beset with sessile lenticular glands mostly 0.05–0.2 mm in diameter (glandular punctate). Leaves opposite. Inflorescence of reduced or expanded dichasia in axils of leaves or bracts, sometimes forming dichasiate spikes, thyrses, or panicles; dichasia alternate or opposite, 1–many-flowered, 1 or more per axil, sessile or pedunculate, subtended by a leaf or a bract. Flowers chasmogamous and/or cleistogamous, homostylous, usually subtended by 2 homomorphic bracteoles (sometimes absent or vestigial). Calyx deeply 5-lobed, lobes homomorphic or heteromorphic. Corolla of chasmogamous flowers blue to blue-purple (in ours, elsewhere also pink, red, white, yellow, or blackish), generally concolorous, tube usually funnelform, often curved, gradually or abruptly expanded distally into a ± distinct throat (rarely saccate), limb 2-labiate (often appearing subactinomorphic), upper lip 2-lobed, lower lip 3-lobed, corolla lobes contorted in bud, corolla of cleistogamous flowers (if present) small and bud-like or tubular, often whitish. Stamens 4, (homodynamous to) didynamous, included in corolla tube or exserted from mouth of corolla, anthers 2-thecous, thecae equal in length, parallel to subsagittate, equally inserted, lacking basal appendages, dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 31) spherical to subspheroidal, 3-porate, exine coarsely reticulate; staminodes 0 or 1. Style included in corolla tube or exserted from mouth of corolla, stigma 2-lobed, lobes equal or unequal, often with 1 lobe greatly reduced, rudimentary, or not evident. Capsule substipitate or stipitate, retinacula present, septa with attached retinacula usually remaining attached to inner wall of mature capsule (separating from inner wall in *R. erythropus*). Seeds 4–28 per capsule, lenticular, pubescent with hygroscopic trichomes (sometimes restricted to margin). ($x = 17$).

Ruellia comprises approximately 250 species worldwide. Species occur primarily in the tropics and subtropics. It is the second largest genus of Acanthaceae in Mexico with about 65 species in the country. The generic synonymy given above only includes genera in which Sonoran species have been treated previously. Ezcurra (1993) provided a more complete list of generic synonyms in which American species have been treated.

1. Corolla white; young stems, leaves, bracteoles, calyx, corolla, and capsule with conspicuous sessile patelliform glands (glandular punctate). . . . . *R. leucantha*
1. Corolla blue; young stems, leaves, bracteoles, calyx, corolla, and capsule lacking sessile patelliform glands (stipitate glands sometimes present, however).
    2. Leaves with at least some trichomes branched or stellate; plants of northeastern Sonora in Chihuahuan desertscrub. . . . . *R. parryi*
    2. Leaves lacking any branched or stellate trichomes; plants not restricted to Chihuahuan desertscrub in northeastern Sonora.
        3. Limb of corolla 10–15 mm in diameter; calyx lobes linear to oblanceolate, unequal with one conspicuously longer and wider than others; thecae 1.7–2.4 mm long; capsule often spotted with red, 7.5–10 mm long, glabrous. . . . . *R. inundata*
        3. Limb of corolla 17–46 mm in diameter; calyx lobes subulate to lance-subulate to linear, equal to subequal; thecae 2.8–5 mm long; capsule never spotted with red, 11–29 mm long, pubescent (sometimes only at apex and inconspicuously so).
            4. Plants woody throughout (shrubs); stipe of capsule 4.5–7.5 mm long; seeds 4 per capsule. . . . . *R. californica*
            4. Plants woody only at or near base (perennial herbs); stipe of capsule 2–4 mm long; seeds 8–20 per capsule.
                5. Those dichasia in axils of distal leaves or leaflike bracts collectively forming a terminal glandular-pubescent paniculiform thyrse; peduncles of distal dichasia, abaxial surface of bracteoles, pedicels, and capsules pubescent with conspicuous glandu-

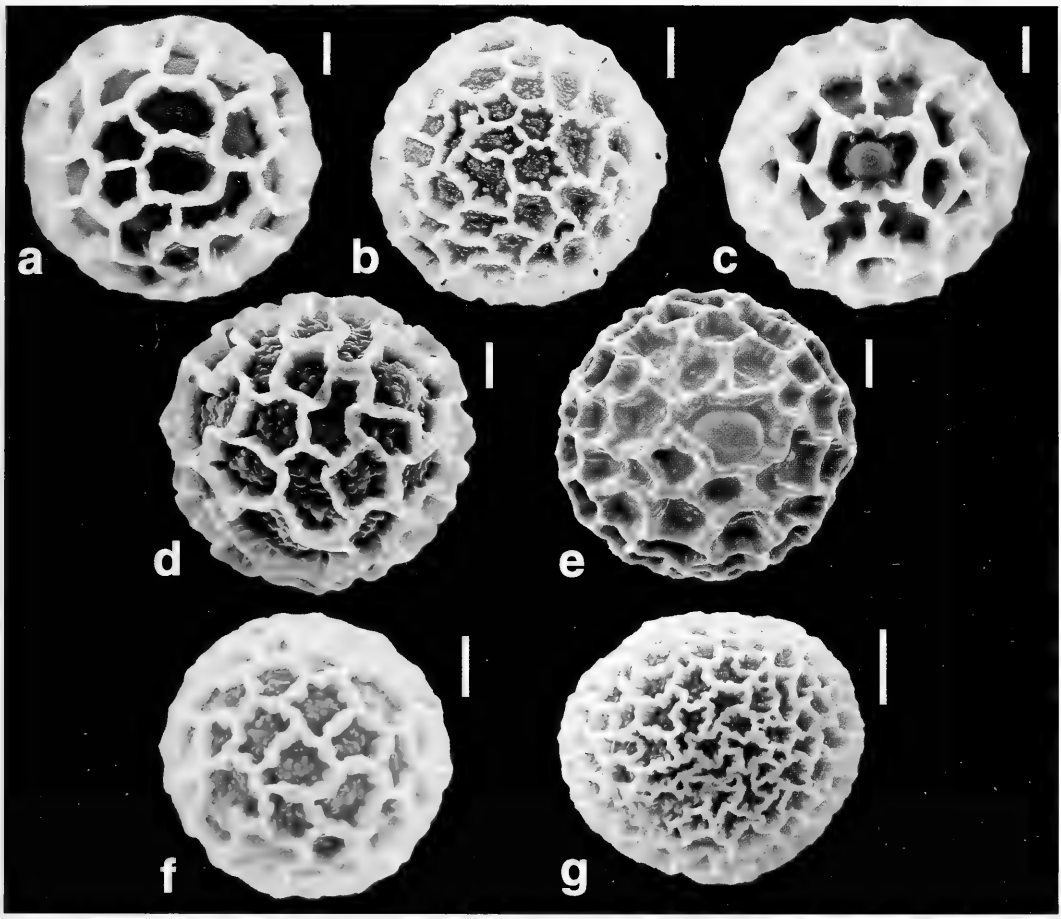


FIGURE 31. Pollen of Sonoran *Ruellia*. a. *R. californica* (*Wiggins 11411*). b. *R. intermedia* (*Jenkins et al. s.n.*). c. *R. inundata* (*Daniel & Butterwick 6952*). d. *R. leucantha* (*Brandegee s.n.*). e. *R. malacosperma* (*Daniel 9773*). f. *R. nudiflora* (*Wiggins & Rollins 136*). g. *R. parryi* (*Reina G. et al. 2003-957*). Scales = 10 μm.

lar trichomes, at least some of which are longer than 0.2 mm; capsule pubescent proximally. . . . . *R. nudiflora*

5. Dichasia pedunculate in axils of leaves, never forming a terminal glandular paniculiform thyrse; peduncles of dichasia, abaxial surface of bracteoles, pedicels, and capsules glabrous or inconspicuously glandular with glandular trichomes up to 0.2 mm long; capsule glabrous proximally.
   6. Leaves 1.1–1.9 times longer than wide, corolla externally pubescent with eglandular trichomes only; style essentially glabrous (sometimes with 1–3 scattered trichomes present); capsule 12–23 mm long, stipe 2–2.5 mm long.. . *R. intermedia*
   6. Leaves 2.3–5.8 times longer than wide; corolla externally pubescent with glandular and eglandular trichomes; style proximally pubescent with eglandular trichomes; capsule 24–29 mm long; stipe 4 mm long. . . . . *R. malacosperma*

Ruellia californica (Rose) I.M. Johnst., Proc. Calif. Acad. Sci., ser. 4, 12:1171. 1924. *Calophanes californica* Rose, Contr. U.S. Natl. Herb. 1:85. 1890. TYPE: MEXICO. Baja California Sur: Santa Rosalía, 24 Feb-3 Mar 1889, *E. Palmer 190* (holotype: US; isotypes: F!, GH!, NY, UC!).

Phenology. Flowering: throughout the year, with a peak in March (Fig. 1); fruiting: throughout the year.

Distribution and habitats. Northwestern Mexico (Baja California, Baja California Sur, Sonora); Sonoran plants occur on slopes and flats in Sonoran desertscrub (Central Gulf Coast, Plains of Sonora), palm oases, and thornscrub at elevations from sea level to 300 m.

Illustrations. Figure 9; *Flora of Baja California*, 194. 1980; *People of the Desert and Sea*, 219. 1985; *Proceedings of the California Academy of Sciences* 49:382. 1997.

Local names. "Hupa chumi" (Yaqui, fide Felger 1999); "rama parda" (fide Felger 1999; Felger and Moser 1985); "satóoml" (Seri, fide Felger and Moser 1985); "stoms" (Seri, *Whiting 9067*).

Uses. A poultice made from the plant is used as a remedy for headache (*Whiting 9067*). Felger and Moser (1985) noted a diversity of uses by the Seri, including: food (nectar sucked from the base of the corolla), medicine (tea made from the leaves ingested for dizziness or headache, put on the face of one who is "tired out" or for dizziness, applied to the eyes as eye drops, and used as a shampoo to relieve headache; tea made from boiling the root (after removal of the epidermis) ingested as a remedy for colds or stuffy nose), and smoking (leaves or corollas dried and smoked in clay pipe to induce hallucinations).

Daniel (1997) provided a description of *Ruellia californica*, which is endemic to northwestern Mexico and attains the northern and eastern extents of its distribution in central and southern Sonora, respectively (Fig. 32). Within the Sonoran Desert of Sonora, the species is especially common in the Central Gulf Coast subdivision near Guaymas. It has been less frequently collected in the Plains of Sonora subdivision. A collection from near Magdalena, about 150 kilometers north of its occurrences in that subdivision, appears to be from the Arizona Upland subdivision. The species is sometimes cultivated, and until *R. californica* is recollected in the Arizona Upland subdivision, its native occurrence there is treated as suspect.

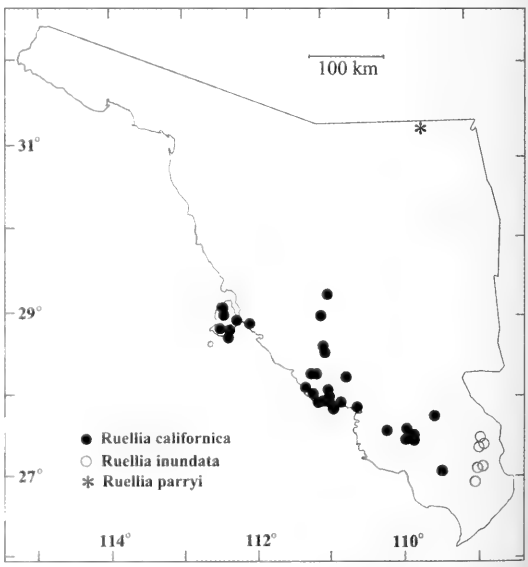


FIGURE 32. Sonoran distributions of *Ruellia californica*, *R. inundata*, and *R. parryi*.

Plants from Sonora are all referable to subspecies *californica* as delimited by Daniel (1997). *Coville 1672* from near Guaymas greatly resembles subsp. *peninsularis* (central and southern Baja California Sur) by the length of its corolla (32 mm), length of its calyx (7 mm), and its glutinous herbage. In this specimen (and similar specimens from this region) there are sparse stipitate glands on the stems and leaves and conspicuous glands on the calyx. These latter characteristics confirm the placement of these plants into subspecies *californica*. An apparently rare occurrence of white corollas among Sonoran plants of this species has been noted (e.g., *Phillips et*

al. 76-183). The herbage is often somewhat viscid and typically mephitic (somewhat skunklike) in odor.

Sonoran collections: Isla Tiburón, *J. Alcocer F. & C. Sosa R. 10* (ENCB); San Carlos Bay, *R. Barr 61-107* (ARIZ); San Francisco Bay near Guaymas, *R. Barr 66-3* (ARIZ); Cerro Bocochibampo, Guaymas, *E. Blakley B-1640* (DS); Guaymas, *T. Brandegee s.n.* (UC); Mpio. Guaymas, 6.5 mi N of road to Bahía San Carlos, ca. 10 mi N of Guaymas on Mex. 15, *D. Breedlove 1464* (DS); Mpio. Hermosillo, 7 mi W of Hwy. 15 along southern paved road to Bahía Kino, *D. Breedlove 15950* (DS, ENCB); Isla Melliza Oeste, near SW end of Guaymas Bay, 27°54′N, 110°54′W, *T. Burgess et al. 6903* (ARIZ); N of Estero El Rancho, 3.9 km N and 1.4 km W of E end of Empalme causeway, 27°59′N, 110°50′W, *T. Burgess et al. 9885* (ARIZ); Sierra Libre, Cañada Tetabejo, S de Hermosillo por la Carr. Fed. 15, 28°33′N, 110°58′W, *A. Búrquez 95-128* (MEXU); La Pintada, 49 km S de Hermosillo, por Carr. Fed. 15, 28°35′N, 110°58′W, *A. Búrquez & D. Yetman 97-431* (MEXU); near San Juan de Guaymas, *A. Carter & D. Noack 4362* (UC); 5 mi S of Guaymas, *G. Chan & J. Folkner s.n.* (ARIZ, MEXU); S Merimar, *O. Clark 14978* (UNM); Guaymas, *F. Coville 1672* (US); ca. 4 mi N of San Carlos at movie site "Catch-22," *T. Daniel 120* (CAS); "Microondas mountain" overlooking Guaymas, *T. Daniel 1963* (ASU, CAS); Nacapuli Canyon, 6.3 mi W of Hwy. 15 toward San Carlos then 4.4 mi N, *T. Daniel 2548* (CAS); W base of Sierra Bojihuacame E of Cd. Obregón, 1.2–2.2 mi SE of Bachoco, *T. Daniel 3366* (CAS, MEXU, NY); ca. 2 mi E of San Carlos, NW of Guaymas, *T. Daniel 3978* (CAS); between San Carlos Bay and Catch-22 airstrip NW of Guaymas, *T. Daniel 3987* (CAS); Guaymas, *E. Dawson 1002* (DS); Isla Tiburón, *R. Delgado B. s.n.* (ENCB); Isla Tiburón *C. Díaz L. 2247* (ENCB); Guaymas, *F. Drouet & D. Richards 3816* (DS, F, US); Isla Tiburón, Ensenada de la Cruz, S end of island, *R. Felger 2589* (ARIZ); Isla Tiburón, SE base of Sierra Kunkaak, *R. Felger 9328* (ARIZ, CAS); Las Guásimas, *R. Felger & R. Devine 85-277* (ARIZ, MEXU); E end, Bahía San Carlos, *R. Felger & C. Lowe 2471* (ARIZ); Isla Tiburón, vic. of Palo Fierro landing field, Punta Tortuga, *R. Felger & A. Russell 8933* (ARIZ, CAS), *Felger et al. 11075* (CAS); road to Bahía San Carlos, 4 mi W of Hwy. 15, *R. Felger & R. Thomas 11917* (ARIZ); ca. 0.5 mi SE of mouth of Nacapule Canyon, ca. 4 mi NE of Bahía San Carlos, *R. Felger & R. Thomas 11954* (ARIZ); Sierra El Aguaje, ca. 18 km NW of San Carlos, ca. 28°03′N, 111°13′W, *R. Felger & M. Wilson 95-238* (ARIZ, CAS); E end of Bahía San Carlos, *R. Felger et al. 10308* (ARIZ); Isla Tiburón, Tecomate, NW part of island, *R. Felger et al. 11126* (ARIZ); Ensenada Grande (= Bahía San Pedro), *R. Felger et al. 12099* (ARIZ); San Carlos Bay, ca. 8 mi N of Guaymas, *R. Ferris 8721* (DS, NY, US); Bahía de Guásimas, just W of Cerro El Bachoco, 15 km E of Empalme, 4.6 mi S of Hwy. 15, 27°54′N, 110°40′W, *M. Fishbein et al. 921* (ARIZ, CAS); Mpio. Guaymas, Sierra El Aguaje, Aguaje Robinson, ca. 10 km NW de San Carlos, 28°03.5′N, 111°07′W, *A. Flores M. & O. Gutierrez R. 5090* (ARIZ, MEXU); N of Magdalena toward Cucurpe, ca. 0.6 mi W of fork, *J. Fryxell 78024A* (TEX); Ciudad Obregón, *H. Gentry 276* (DS, US); Mutica, Río Yaqui, *H. Gentry 2193* (F, MO); Bachoco, 12 mi E of Cajeme, *H. Gentry 2973* (ARIZ, MEXU, S); Guaymas, *H. Gentry 4710* (ARIZ); Isla Tiburón, *D. Gold 386* (MEXU); 1 mi E of Bahía San Carlos, ca. 12 mi N of Guaymas, *B. Hansen et al. 1389* (LL, MEXU, US, WIS); 10.2 mi N of turnoff to Bahía San Carlos, *J. Hastings & R. Turner 64-18* (ARIZ, DS); ca. 35 mi N of Guaymas and 7 mi W of Hwy. 15 toward Kino Bay, *J. Hastings & R. Turner 65-160* (ARIZ, DS); 2 mi N of San Carlos Bay, *P. Hutchison 2447* (MEXU, US); ca. 18 mi N of Hermosillo, *E. Jaeger 5* (DS); island in bay near Guaymas, *I. Johnston 3088* (CAS); Tiburón Island, *I. Johnston 4268* (CAS, NY, UC, US); Ensenada Grande (San Pedro Bay), *O. Kleine et al. 11588* (ARIZ); Tiburón Island, *Knight et al. 1101* (UNM); 70 mi S of Hermosillo, *G. Lindsay 1134* (DS); Isla Tiburón, *E. Lott & T. Atkinson 2513* (CAS), *2514* (CAS); road to Bahía San Carlos, *C. Lowe & R. Felger 1671* (ARIZ); Algodones Bay area, 4 mi WNW of San Carlos Bay, *P. Martin s.n.* (ARIZ); Guaymas, Microwave Mountain, 27°57', 110°54′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); N de Guaymas, *F. Miranda 8945* (MEXU); Ardilla Island, Guaymas Harbor, 27°55′N, 110°54′W, *R. Moran 4020* (DS); Tiburón Island, 28°46′N, 112°18′W, *R. Moran 4059* (DS, UC); Tiburón Island, Arroyo de la Cruz, 28°46′N, 112°22′W, *R. Moran 13005* (ARIZ, CAS); Isla Tiburón, Arroyo Sauzal, S end of island, *E. Moser & M. Moser s.n.* (ARIZ); ca. 18 mi S of Guaymas, *D. Norris et al. 20057* (CAS, MEXU); Guaymas, *E. Palmer 196* (C, NY, UC, US); near Guaymas, *W. Palmer 1222* (US); 6–8 mi NE of Cajeme (Cd. Obregón), *F. Pennell 19470* (MEXU, PH, US); entrance to Nacopuli Canyon, 3 mi N of San Carlos Bay, *A. Phillips et al. 75-175* (UC); Nacopuli Canyon road, 4.5 mi N of San Carlos Bay, *A. Phillips et al. 76-183* (ARIZ, CAS); Rte. 15, ca. 5 mi N of Navojoa, *D. Pinkava et al. P12928* (ARIZ); Ensenada Chica, 15.1 mi W of Hermosillo to Guaymas Hwy., 28°07′N, 111°17′W, *F. Reichenbacher 224* (ARIZ); Mpio. Empalme, Rancho las

Trincheras, ca. 6 km NW of Empalme, 28°01′N, 110°50′W, *A. Reina G. & T. Van Devender 2001-182B* (CAS); camino Bahía de Kino–Punta Chueca, KM 16.3, 28°55′N, 112°02′W, *A. Reina et al. 95-62* (ARIZ, CAS); Mpio. Guaymas, 27.4 km S of Restaurant Los Arrieros, KM 143 on Mex. 15, 28°05′N, 110°57′W, *A. Reina G. et al. 98-01* (CAS, MEXU, TEX); Guaymas, Colonia Peninsular, *H. Ripley 14266* (NY); Tiburón Island, *J. Rose 16790* (US); vicinity of Guaymas, *J. Rose et al. 12585* (US); vicinity of Empalme, *J. Rose et al. 12626* (NY, US); vicinity of Bahía San Carlos, *J. Russell s.n.* (ARIZ); near Rancho El Valiente, Hwy. 15 at jct. with bypass to Cd. Obregón, 3.8 mi N of turnoff to San Carlos Bay, ca. 28°02′N, 110°56′W, *A. Sanders et al. 8766* (CAS, MO); Isla Tiburón, 3 km W Punta Tormenta, *N. Scott P5* (UNM); near Ortiz, *F. Shreve 6104* (ARIZ, F); San Carlos Bay, W of Guaymas, *F. Shreve 6408* (ARIZ, F); 17 mi S of Guaymas on Mex. 15, *W. Spaulding 75-3-32* (ARIZ); 3 mi E of Mex. 15 on road to La Pintada Canyon, 28°35.5′N, 110°58.5′W, *G. Starr 754* (ARIZ); 5.8 mi N of turnoff to Bahía San Carlos on Mex. 15, *G. Starr & D. Palzkill 290* (ARIZ); Nacopuli Canyon near Bahía San Carlos, *G. Starr & C. Starr 713* (ARIZ); entrance to Nacopuli Canyon, *G. Starr et al. 27* (ARIZ); near Hwy. 15 ca. 12.2 mi E of Vicum Station, *W. Stevens 1506* (ENCB, MO); Isla Tiburón, Ensenada de Perros, 28°46′N, 112°16′W, *P. Tenorio L. et al. 9523* (F, MEXU); Tiburón Island, Sau Sal drainage, S side of island, *Tewksbery et al. s.n.* (ARIZ); Isla Tiburón, *F. Torres s.n.* (ENCB); 2.3 mi NW of Guaymas, *R. Turner & C. Lowe 148* (ARIZ); 7.5 mi W of jct. with Mex. 15, along Kino Bay Road cutoff, 28°17′N, 110°08′W, *R. Van Devender & T. Van Devender 83-116* (ARIZ); Cañón Babiso, Rancho Babiso, 2.5 mi W of San Carlos Bay, *T. Van Devender & M. Kearns s.n.* (ARIZ); Nacopuli Canyon, ca. 4 mi N of San Carlos Bay, *T. Van Devender et al. 84-238* (ARIZ); 10.2 mi W of Mex. 15 toward El Sahuaral (southern road to Bahía Kino), 28°19′N, 110°12′W, *T. Van Devender et al. 92-11* (ARIZ, CAS); Canada El Tetabejo, Sierra Libre, 28°32.5′N, 110°59′W, *T. Van Devender et al. 95-1042* (ARIZ); 75 mi S of Hermosillo on Hwy. 15, *J. Walker 98* (TEX); 1 mi N of Las Guásimas, 19 mi S of Guaymas along Mex. 15, 27°55′N, 110°34′W, *R. Warren & D. Goldberg s.n.* (ARIZ); ca. 15 mi SE of Guaymas, *G. Webster & S. Lynch 17003* (MEXU, MO); Tiburón Island, vicinity of Tecomate on N shore of island, *A. Whiting 9067* (ARIZ); 3 mi S of Ortiz toward Guaymas, *I. Wiggins 6324* (DS, UC, US); Isla Tiburón, La Sauzal, 28°49′N, 112°35′W, *I. Wiggins 17174* (DS, MEXU); Coralitos, shore at S side of Isla Tiburón, *R. Wilkinson 193* (MEXU); 10 mi NW of Bahía San Carlos, *N. Yensen 740319-1* (ARIZ).

Ruellia intermedia Leonard, J. Wash. Acad. Sci. 17:512. 1927. TYPE: MEXICO. Jalisco: Bolaños, 10–19 Sep 1897, *J. Rose 2915* (holotype: US!; isotype: NY!).

Phenology. Flowering: July–September; fruiting: August–October, February–March.

Distribution and habitats. Mexico (Baja California Sur, Chiapas, Chihuahua, Colima, Guerrero, Jalisco, México, Michoacán, Morelos, Nayarit, Sinaloa, Sonora); Sonoran plants occur in Sonoran desertscrub (Plains of Sonora), thornscrub, tropical deciduous forests, and in mesquite bosques along streams at elevations from 120 to 1000 m.

Illustration. *Journal of the Washington Academy of Sciences* 17:513. 1927.

Local names. "Conivari" (Pima, *Pennington 249*); "papachili" (Mayo, fide Van Devender et al. 2000); "rama del toro" (*Salmon s.n.*); "suspinda" (Pima, *Pennington 249*); "trikis sípunim" (Pima Bajo, *Rea 1154*); "tronando" (*Rea 1154*); "yerba del toro" (fide Gentry 1942, as *R. tuberosa*).

Use. The seeds are used in preparing a "refreshing drink-soak" (*Pennington 249*).

Daniel (1995a, 1997) provided descriptions of this species, which reaches the northern and western extents of its distribution in north-central Sonora (Fig. 33). Although most collections were made in thornscrub and tropical deciduous forest, a few collections have been made in regions of Sonoran desertscrub. Among Sonoran plants, the calyces are pubescent with mostly glandular trichomes (e.g., *Van Devender et al. 98-1276*), pubescent with exclusively eglandular trichomes (e.g., *Reina G. et al. 98-862* and most collections), or nearly glabrous (e.g., *Van Devender et al. 94-654A*). *Trauba s.n.* contains a shoot with glandular pubescent calyces and other shoots with calyces lacking glandular trichomes; *Daniel 993* shows both glandular- and eglandular-pubescent calyces on the same plant.

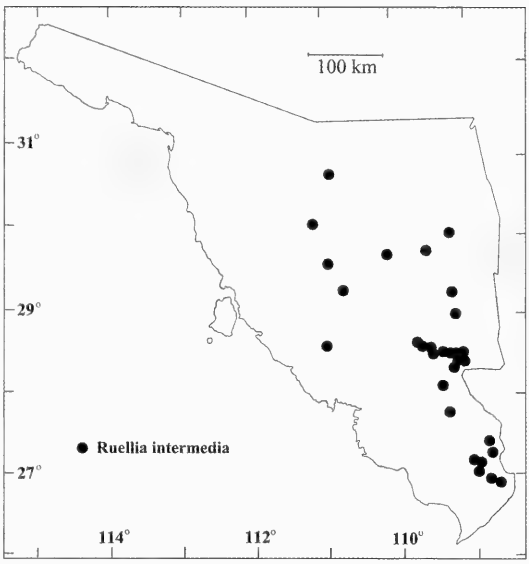


FIGURE 33. Sonoran distribution of *Ruellia intermedia*.

SONORAN COLLECTIONS: Mpio. San Javier, 2.7 km E of La Barranca on Mex. 16, 28°34′N, 109°40′W, *A. Búrquez M. 96-261* (CAS); between Onavas and hwy. between Esperanza and Rosario de Tezopaco, 5 mi S of Movas, *T. Daniel 993* (CAS); El Coyote, E-central Sonora, *R. Felger 3571* (ARIZ); Mpio. Guaymas, Sierra Libre, Cañón Tetabejo, 28°32′N, 110°59′W, *R. Felger et al. 02-292* (CAS); ca. 1 km S of El Tabelo on Alamos–San Bernardo road, 27°09′N, 108°58′W, *M. Fishbein et al. 1872* (ARIZ, CAS); Arroyo Seco, SW of Los Camotes along Los Tanques–Las Chinacas road, 27°16′N, 108°51′W, *M. Fishbein et al. 1880* (ARIZ); Dist. Alamos, Canyon Estrella, *H. Gentry 353* (DS); highway between Alamos and Navojoa, *A. Gibson & L. Gibson 2081* (ENCB, TEX); 4.3 km SW of Santa Ana de Yécora on road to Nuri, 28°23′N, 109°19′W, *D. Goldberg & S. McLaughlin 77-173* (ARIZ); Lo de Campo, near San Xavier mine turnoff on Hwy. 16, Río Mayo region, *P. Martin et al. s.n.* (ARIZ); Arroyo Gochico, E of San Bernardo, *F. Pennell 19516* (GH); Onavas, *C. Pennington 249* (TEX); NE of Onavas at mine, 28°28′N, 109°32′W, *A. Rea 1154* (ARIZ); Mpio. Onavas, Rancho la Mula, 5 km W of Agua Amarilla, 28.2 km SE of Río Yaqui on Mex. 16, 28°29′N, 109°22′W, *A. Reina G. 97-576* (CAS); Mpio. Yécora, Arroyo Santa Ana at SON. 12, 8.5 km W of Guadalupe Tayopa, 28°21′N, 109°16′W, *A. Reina G. et al. 98-862* (CAS); Mpio. Yécora, Arroyo La Quema, near Tepoca, 28°26′N, 109°15′W, *A. Reina G. et al. 98-871* (CAS, MEXU); Mpio. Soyopa, near Arroyo Garambullo on NE side of Río Yaqui bridge on Mex. 16, just S of Tonichi, ca. 28°34′N, 109°33′W, *A. Reina G. et al. 99-33* (CAS); Mpio. Yécora, base of Cerro El Pilar, above Arroyo Santa Ana, 5.5 km N of Curea on Son. 12, 28°20′N, 109°15′W, *A. Reina G. et al. 99-797* (CAS); Mpio. Sahuaripa, 8 km N of Río Yaqui, 25.5 km N of Sahuaripa on road to Tepache, 29°15′N, 109°19′W, *A. Reina G. et al. 2003-933* (CAS); 7 mi N of Guirocoba, *J. Salmon s.n.* (ARIZ, CAS); Mpio. Alamos, Rancho Esmeralda, NW outskirts of Alamos toward San Bernardo, 27°02′N, 108°56′W, *A. Sanders et al. 12501* (CAS); 7 mi S of Baviácora, *F. Shreve 6734* (ARIZ, UC); 190 km E of Hermosillo on Yécora, *P. Sundt s.n.* (ARIZ); Rancho El Carrizo, 100 mi S of Nogales, *R. Tomelson s.n.* (ARIZ); Mpio. Yécora, 1.6 km E of Rancho Viejo toward Santa Ana, ca. 28°20′N, 109°15′W, *W. Trauba s.n.* (CAS); Alamos, 27°01′N, 108°50′W, *T. Van Devender 94-619* (ARIZ); Mpio. Onavas, Rancho La Mula, 28.2 km SE of Río Yaqui on Mex. 16 (KM 195 E of Hermosillo), 28°28.5′N, 109°22′W, *T. Van Devender & A. Reina G. 2000-509* (ARIZ); Mpio. Soyopa, Loma Maderista, 3.5 km S of Tonichi, ca. 28°34′N, 109°33′W, *T. Van Devender & A. Reina G. 2001-200* (CAS); Mocuzari (Adolfo Ruiz Cortinez) Dam on Río Mayo, WNW of Alamos, 27°13′N, 109°06.5′W, *T. Van Devender & R. Van Devender 92-1385* (ARIZ, CAS); Las Lajitas crossing of the Río Cuchujaqui, 8.9 mi ESE of Alamos, 26°59′N, 108°49′W, *T. Van Devender et al. 92-1377* (CAS); El Rincon Viejo, ca. 4 km N of Alamos, Sierra de Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 94-654* (ARIZ), *94-654A* (ARIZ, TEX); Mpio. Yécora, Curea, 28°19′N, 109°17′W, *T. Van Devender et al. 98-1276* (CAS); Mpio. Arivechi, Arroyo Agua Caliente, 10.2 km (air) WNW of Arivechi, 28°57′N, 109°17′W, *T. Van Devender et al. 99-880* (CAS); Mpio. Yécora, Rancho La Palma Agujerada, 7.1 km N of Mex. 16 on road to Sahuaripa, 28°28.5′N, 109°11′W, *T. Van Devender et al. 2000-359* (ARIZ); Mpio. Moctezuma, 20.5 km SSE jct. with Moctezuma–Huasabas hwy. on road to Tepache (Son. 117), 29°39′N, 109°35′W, *T. Van Devender et al. 2004-413* (CAS); Mpio. San Javier, Cerro el Halcon, near San Javier, 28°37′N, 109°43′W, *L. Varela E. 96-209B* (CAS); ca. 1 mi E of RR on road to Horcasitas, *I. Wiggins 7275* (ARIZ, DS, GH, MICH, US); E slope of Sierra Batuc, several mi NW of Batuc, *I. Wiggins & R. Rollins 292* (ARIZ, DS, GH, MO, UC, US), *292a* (DS).

Ruellia inundata H.B.K., Nov. Gen. Sp. 2:239. 1817. *Aphragmia inundata* (H.B.K.) Bremek., Verh. Kon. Ned. Akad. Wetensch. Afd. Natuurk., Tweede Sect. 45:10. 1948. TYPE: COLOMBIA. "In ripa fluminis Magdalenae prope Mompox et Badillas," May, (fide protologue), *A. von Humboldt & A. Bonpland mss. n. 3711* (holotype: P-Bonpl.!).

Ruellia albicaulis Bertero ex Spreng., Syst. Veg. 2:822. 1825. TYPE: COLOMBIA. "Ad fl. Magdalen." (fide protologue), no specimens have been seen.

Aphragmia haenkei Nees in Lindley, Intr. Nat. Syst. Bot., ed. 2, 444. 1836. *Dipteracanthus haenkei* (Nees) Nees in A. de Candolle, Prodr. 11:141. 1847. TYPE: MEXICO. Guerrero: Acapulco, 1791, *T. Haenke s.n.* (no type designated nor place of deposition noted; probable type material: K, PR!, PRC!).

Ruellia galeottii Leonard, Kew Bull. 1938:59. 1938. TYPE: MEXICO. Oaxaca: Sola, Oct 1844, *H. Galeotti 510J* (holotype: US!; isotypes: NY!, W!).

Phenology. Flowering: October–April; fruiting: October–April.

Distribution and habitats. Mexico (Baja California Sur, Campeche, Chiapas, Colima, Guerrero, Jalisco, México, Michoacán, Morelos, Oaxaca, Puebla, Quintana Roo, Sinaloa, Sonora, Veracruz, Yucatán), Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Ecuador, and Brazil; Sonoran plants occur in canyons and disturbed sites in tropical deciduous forests at elevations from 260 to 740 m.

Illustrations. *Carnegie Institution of Washington Publication* 461:210. 1936; *Fieldiana, Botany* 18:17. 1986.

Descriptions of *Ruellia inundata* were provided by Daniel (1995a, 1997). Sonoran plants are noted as having bluish corollas. Vegetative organs of plants of this species are usually viscid and have a mephitic odor (similar to that of *Dyschoriste hirsutissima*). The species reaches the northern extent of its distribution in southern Sonora (Fig. 32).

Sonoran collections: San Bernardo, Río Mayo, *H. Gentry 1068* (ARIZ, F, MO, S, US); near Tojibampo, 19.5 km NNW of San Bernardo toward Mesa Colorada, 27°02′N, 108°47′W, *T. Van Devender et al. 93-369* (ARIZ, CAS, TEX), *93-1495* (ARIZ, CAS, MO, NY, TEX), *93-1495A* (ARIZ); ca. 4 km NNW of Nahuibampo, W slopes of Cordón Topiyecas, 27°24′N, 108°55′W, *T. Van Devender et al. 94-353* (ARIZ); western Sierra de Alamos, 7.7 km S of Tetajiosa toward Las Rastras, 26°56′N, 109°04′W, *T. Van Devender et al. 95-158* (ARIZ, CAS); Cerro las Tátemas, below Microondas La Luna, 13.8 km NW of Alamos, 27°07′N, 109°02′W, *T. Van Devender et al. 95-1158* (ARIZ, CAS); 4.7 km SSE of Piedras Verdes toward Tepustete, ca. 12 km NNW of Alamos, 27°08′N, 108°56′W, *T. Van Devender et al. 95-1180* (CAS).

Ruellia leucantha Brandegee subsp. ***postinsularis*** (Gentry) T.F. Daniel, Polibotanica 2:7. 1996. *Ruellia leucantha* var. *postinsularis* Gentry, Brittonia 6:323. 1948. TYPE: MEXICO. Sinaloa: Cerro Tecomate, W of Pericos, 28 Feb 1940, *H. Gentry 5739* (holotype MICH!; isotypes ARIZ, DS!, GH, MEXU!, MO, NA, NY, RSA!, UC!, US).

Dyschoriste candida Brandegee, Zoe 5:242. 1906. *Ruellia candida* (Brandegee) Kobuski, Ann. Missouri Bot. Gard. 15:60. 1928. TYPE: MEXICO. Sinaloa: vicinity of Culiacán, Yerba Buena near Altata, 10 Oct 1904, *T. Brandegee s.n.* (holotype UC!; isotypes GH!, US!).

Shrubs to 8 dm tall. Young stems quadrate to quadrate-sulcate, evenly puberulent with erect to flexuose to retrorse eglandular trichomes 0.05–0.2 mm long and sessile patelliform glands (glandular punctate), the trichomes sometimes very dense and ± obscuring epidermis. Leaves petiolate, petioles to 7 mm long, blades ovate to elliptic, 22–57 mm long, 11–33 mm wide, 1.7–2.2 times longer than wide, rounded to acute at apex, rounded to subattenuate at base, surfaces glandular punctate and pubescent (sometimes very densely so) with erect to flexuose to antrorse eglandular

trichomes 0.1–0.5 mm long, margin ciliate with similar trichomes. Inflorescence of axillary dichasia; dichasia sessile, 1 (–2) per axil, 1-flowered, alternate or opposite at vegetative nodes; flowers sessile to subsessile (i.e., borne on pedicels to 1 mm long). Bracteoles prominent to inconspicuous (to obsolete), sometimes caducous, petiolate and linear-elliptic to linear or sessile and triangular to triangular-subulate, 0.2–23 mm long, 0.2–5 mm wide, pubescent like young stems. Calyx 5-lobed, (5–) 7–14 mm long, tube 1–2 mm long, lobes subulate to linear-subulate, subequal to unequal in length (i.e., 1 lobe up to 1 mm longer than others), (4–) 6.5–13 mm long, 4–8.3 times longer than tube, abaxially pubescent like young stems. Corolla white, 38–68 mm long, externally glandular punctate and pubescent with erect to flexuose to retrorse eglandular trichomes 0.1–0.3 mm long, tube funnelform, 40–52 mm long, 2.2–3 mm in diameter near midpoint, narrow proximal portion of tube 17–30 mm long, distally abruptly expanded into a throat 13–23 mm long, limb (22–) 37–40 mm in diameter, lobes 7–16 mm long, 8–16 mm wide. Stamens included to ± exserted, didynamous, longer pair 12–18 mm long, shorter pair 10–16 mm long, filaments proximally pubescent with eglandular trichomes and glandular punctate, distally glabrous, thecae (3–) 4.5–5.5 mm long. Style (25–) 33–47 mm long, pubescent with erect to antrorse eglandular trichomes and glandular punctate; stigma unequally 2-lobed, 1 lobe 2–2.8 mm long, other lobe 0.2–0.4 mm long. Capsule 8–12 mm long, externally glandular punctate and pubescent with erect to flexuose to retrorse eglandular trichomes 0.05–0.2 mm long, stipe 2 mm long, head ovoid ellipsoid to ellipsoid-subcircular, 8–10 mm long. Seeds 4 (–6) per capsule, 3.5–4.5 mm long, 3.2–4.5 mm wide, surfaces and margin covered with appressed hygroscopic trichomes to 0.3 mm long, margin ± swollen.

Phenology. Flowering: August; fruiting: April, October.

Distribution and habitats. Northwestern Mexico (Sinaloa, Sonora); Sonoran plants occur in desert oases in riparian Sonoran desertscrub (Plains of Sonora) at elevations from 250 to 300 m.

Illustration. None found.

The collections cited below represent the first records of this species in Sonora. Daniel (1996, 1997) recognized two subspecies of *Ruellia leucantha*. Plants from Sonora pertain to *R. leucantha* subsp. *postinsularis* and greatly resemble the type from Sinaloa. The description of that subspecies provided by Daniel (1996) has been augmented with data from Sonoran plants and is provided above. The nominate subspecies is restricted in distribution to the Cape Region of Baja California Sur (Daniel 1997). The subspecies of *R. leucantha* can be distinguished by the following couplet:

1. Cauline trichomes erect to flexuose, 0.3–1.5 mm long; capsules 12–15 mm long; Baja California Sur. . . . . subsp. *leucantha*
1. Cauline trichomes erect to retrorse, 0.05–0.2 mm long; capsules 9–12 mm long; Sonora and Sinaloa. . . . . subsp. *postinsularis*

The northern distributional extents of both the species and subspecies *postinsularis* are in west-central Sonora (Fig. 30). The collector of all known Sonoran plants of *R. leucantha* noted that the desert oasis in which the species occurs in that state is located in a region of deep canyons (with permanent water) in which numerous tropical species occur. Its occurrence within the Sonoran Desert, like that of *Aphanosperma sinaloensis*, is restricted to riparian corridors in which more tropical elements extend their ranges. According to T. Van Devender (pers. commun.), the canyon slopes are dominated by thornscrub.

Some confusion with respect to corolla color is present among the label data on Sonoran collections of this species. The sole flowering specimen (*Búrquez & Yetman 97-431*), identified as *R. californica*, notes that corollas were purple (i.e., as in *R. californica*). A fruiting collection (*Búrquez et al. 97-497*), identified as *Justicia candicans*, noted that corollas were red (i.e., as in *J. candicans*). I suspect that corolla colors as provided on the labels of these collections pertain to the

species as identified, not to the plants collected. If I am incorrect, and Sonoran representatives of *R. leucantha* do not have white corollas like their counterparts in Sinaloa and Baja California Sur, then the glandular punctate pubescence still distinguishes this species from other Sonoran *Ruellia*.

Sonoran collections: La Pintada, 49 km S de Hermosillo por la Carr. Fed. 15, 28°35′N, 110°58′W, *A. Búrquez & R. Felger 93-32* (MEXU), *A. Búrquez & D. Yetman 97-431* (MEXU); Sierra Libre, Cañada Prieta, S de Hermosillo por la Carr. Fed. 15, 28°34′N, 110°58′W, *A. Búrquez et al. 97-497* (MEXU).

Ruellia malacosperma Greenm., Proc. Amer. Acad. Arts 34:572. 1899. TYPE: MEXICO. Tamaulipas: Tampico, 30 Apr 1898, *C. Pringle 6806* (lectotype, designated here, see discussion below: GH, photo at CAS!; isolectotypes: BM!, F!, L!, LL, MEXU, MIN!, NSW!, NY, PR!, PRC!, S!, UC!, US).

Perennial herbs to 1 m tall. Young stems quadrate to quadrate-sulcate to ± flattened, internodes mostly glabrous or sometimes ± evenly pubescent with flexuose eglandular trichomes 0.5–2 mm long, nodes pubescent with flexuose eglandular trichomes 0.5–2 mm long. Leaves petiolate, petioles to 20 mm long, blades narrowly elliptic to elliptic, 45–163 mm long, 8–38 mm wide, 2.3–5.8 times longer than wide, (rounded to) acute to attenuate at apex, acute to attenuate at base, surfaces sparsely pubescent with a few scattered flexuose eglandular trichomes along midvein, midvein conspicuously caniliculate on adaxial surface (at least near proximal portion of blade), margin subsinuate to crenate-undulate. Inflorescence of pedunculate ascending expanded dichasia to 120 mm long from leaf axils; dichasia (opposite to) alternate, 1 per axil, (1–) 3–many-flowered, peduncles 26–70 mm long, subquadrate to quadrate, glabrous or sparsely pubescent with inconspicuous glandular trichomes 0.05–0.1 mm long (glandular-puberulent). Bracteoles sometimes caducous, lanceolate to lance-linear, 5–10 mm long, 1–1.5 mm wide, abaxial surface glabrous, secondary bracteoles similar to bracteoles except smaller. Flowers pedicellate, pedicels 4–12 mm long, ± densely glandular-puberulent. Calyx 13–21 mm long, tube 2–3 mm long, lobes lance-subulate, subequal (i.e., longest lobe 1.1–1.3 times longer than shortest lobe), 10.5–18 mm long, 3.8–7.5 times longer than tube, 1.2–1.5 mm wide, abaxially glandular-puberulent (glands up to 0.2 mm long), margin ciliate with antrorse eglandular trichomes 0.05–0.6 mm long and/or glandular-puberulent. Corolla blue-purple, 45–60 mm long, externally pubescent with flexuose eglandular and glandular (sometimes sparse) trichomes 0.1–0.2 mm long, tube 33–38 mm long, narrow proximal portion 9–15 mm long, ± abruptly expanded into throat, throat 18–25 mm long, longer than narrow proximal portion, 6.5–14 mm in diameter near midpoint, limb 32–46 mm in diameter, lobes 12–17 mm long, 14–18 mm wide. Stamens included, longer pair 12–15 mm long, shorter pair 8–10 mm long, thecae 3.7–4 mm long. Style 20–21 mm long, pubescent (at least proximally) with upward-pointing eglandular trichomes, stigma unequally 2-lobed, 1 lobe 0.2 mm long, other lobe 1.5–2.2 mm long. Capsule 24–29 mm long, proximally glabrous, inconspicuously pubescent near apex with erect to antrorse glandular and eglandular (sometimes absent) trichomes 0.05–0.2 mm long, stipe 4 mm long, head linear-ellipsoid. Seeds 16–20 per capsule, 3.1–3.2 mm long, 2.4–2.5 mm wide, surfaces and margin covered with appressed hygroscopic trichomes.

Phenology. Flowering: June, October; fruiting: March, June, October.

Distribution and habitats. Presumably native to Mexico where it has been recorded from Guerrero, Nuevo León, San Luis Potosí, Sinaloa, Tamaulipas, and Veracruz (reports from some of these states undoubtedly are based on cultivated plants); Sonoran plants are cultivated or occur in margins of dried pools in coastal thornscrub with *Prosopis, Acacia, Cyperus*, and *Lycium* at elevations near sea level (naturalized or possibly native plants) or up to 415 m (cultivated plants).

Illustration. *Carnegie Institution of Washington Publication* 461:208. 1936.

Three collections, from three Mexican states, were cited by Greenman in the protologue:

Pringle 6806 (Tamaulipas), *Palmer 570* (Guerrero), and *Botteri s.n* (Veracruz). The latter collection was cited somewhat incidentally, and it was noted to be at GH. Although their herbaria of deposit were not noted in the protologue, specimens of both *Palmer 570* and *Botteri s.n.* have been located to date only at GH. Pringle's collection was widely distributed with a printed label bearing Greenman's name for this taxon. It remains unknown, however, whether Greenman actually studied all of the duplicates. Therefore, only the specimens at GH of these three collections are here considered to be syntypes. Tharp and Barkley (1949) indicated that the "type" of *R. malacosperma* was *Pringle 6806*. This would appear to be sufficient under the current International Code of Botanical Nomenclature (Greuter 2000) to effectively lectotypify the species (i.e., with the only syntype of *Pringle 6806* being at GH). If it is argued, or can be demonstrated, that Greenman used duplicates of this collection in composing his protologue, then this would not appear to have constituted a valid lectotypification under Article 7.11 of the ICBN because the "type element" is not clearly indicated (i.e., there are numerous syntypes of *Pringle 6806*). To avoid further confusion, *Pringle 6806* at GH, a complete specimen with flowers and fruits, is here designated as the lectotype for this species. It is likely that Tharp and Barkely's "lectotypification" was unintentional and that mine is superfluous, but neither rationale would prevent the lectotypification of this name under the ICBN.

This species is cultivated in Sonora (e.g., *Daniel 9773*) and either escapes/naturalizes or is also native to the state (e.g., *Sanders et al. 13579*). There is no indication on *Rose 1288* whether the plant was cultivated or not in Guaymas. The above description is based on the type and other Mexican collections resembling it. *Sanders et al. 13579*, consisting of fruiting rhizomatous plants collected in March in thorn scrub, resembles *R. malacosperma* in most respects and is tentatively treated in that taxon. Corollas are not present on this collection, however, and it differs from others of *R. malacosperma* by its lower stature (2 vs. up to 10 dm tall), shorter leaves (20–50 vs. 45–135 mm long), shorter inflorescences (e.g., peduncles 2–7 vs. 30–65 mm long), and shorter capsules (15–18 mm long). Although the distinctions between *R. malacosperma* and *R. coerulea* Morong are not great (Daniel 1995a; Turner 1991-with *R. coerulea* treated as *R. brittoniana* Leonard), specimens from Sonora more closely resemble the former rather than the latter taxon by their relatively wider (2.9–6.2 times longer than wide) leaf blades (vs. 5.6–30 times longer than wide in *R. coerulea*). Both species are widely cultivated, and their origins and/or native distributional ranges are not known with certainty.

Sonoran collections: garden of La Ciudadela just off Plaza de Armas in Alamos, ca. 27°01′N, 108°56′W, cultivated, *T. Daniel 9773* (CAS); Mpio. Huatabampo, roadside ca. 1 km N of Maroncarit, 10 km NW of Yavaros, ca. 26°44′N, 109°37′W, *A. Sanders et al. 13579* (ARIZ, CAS, MO); Guaymas, *J. Rose 1288* (US).

Ruellia nudiflora (Engelm. & A. Gray) Urb., Symb. Antill. 7:382. 1912. *Dipteracanthus nudiflorus* Engelm. & A. Gray, Boston J. Nat. Hist. 5:229. 1845. TYPE: UNITED STATES. Texas: Sim's Bayou near Houston, May–Jul (fide protologue) 1843, *F. Lindheimer 157* (lectotype, designated here, see discussion below: GH!; isolectotypes: GH!, UC!).

Ruellia tuberosa L. var. *occidentalis* A. Gray, Syn. Fl. N. Amer. 2(1):325. 1878. *Ruellia nudiflora* var. *occidentalis* (A. Gray) Leonard, J. Wash. Acad. Sci. 17:516. 1927. *Ruellia occidentalis* (A. Gray) Tharp & F.A. Barkley, Amer. Midl. Naturalist 42:25. 1949. TYPE: collections of Berlandier, Wright, Rothrock, and Coulter from the southwestern United States were cited by Gray; Leonard (J. Wash. Acad. Sci. 17:516. 1927) indicated that the type was collected in Texas by Berlandier; it will require study of these collections to determine whether Leonard effectively lectotypified the species at that time.

Ruellia nudiflora var. *glabrata* Leonard, J. Wash. Acad. Sci. 17:518. 1927. *Ruellia glabrata* (Leonard) Tharp & F.A. Barkley, Amer. Midl. Naturalist 42:13. 1949. TYPE: MEXICO. Sonora: Ciénega, Aug 1874, *J. Rothrock 560* (holotype: US; isotypes: GH!, NY).

Ruellia gooddingiana A. Nelson, Amer. J. Bot. 18:437. 1931. TYPE: MEXICO. Sonora: La Ciénega, 18 Jul 1911, *L. Goodding 959* (holotype: RM!).

See Daniel (1995a) for a complete listing of synonyms for this species.

Phenology. Flowering: March, July–October; fruiting: July–October.

Distribution and habitats. United States (Arizona, Louisiana, Texas), Mexico (Baja California Sur, Campeche, Chiapas, Chihuahua, Coahuila, Colima, Durango, Morelos, Nuevo León, Oaxaca, Puebla, Querétaro, Quintana Roo, San Luis Potosí, Sinaloa, Sonora, Tabasco, Tamaulipas, Veracruz, Yucatán), Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, and West Indies; Sonoran plants occur in swampy meadows, flats, swales, along watercourses, and in disturbed areas in Sonoran desertscrub (Arizona Upland, Central Gulf Coast, Lower Colorado River Valley, Plains of Sonora), Chihuahuan desertscrub, palm oases, thornscrub, mesquite grasslands, mesquite bosques, and tropical deciduous forests at elevations from near sea level to 1180m.

Illustrations. Figure 34; *Carnegie Institution of Washington Publication* 461:211. 1936; *Flora of Texas* 1(3):240. 1966; *Desert Plants* 5:172. 1984; *Fieldiana, Botany* 18:18. 1986.

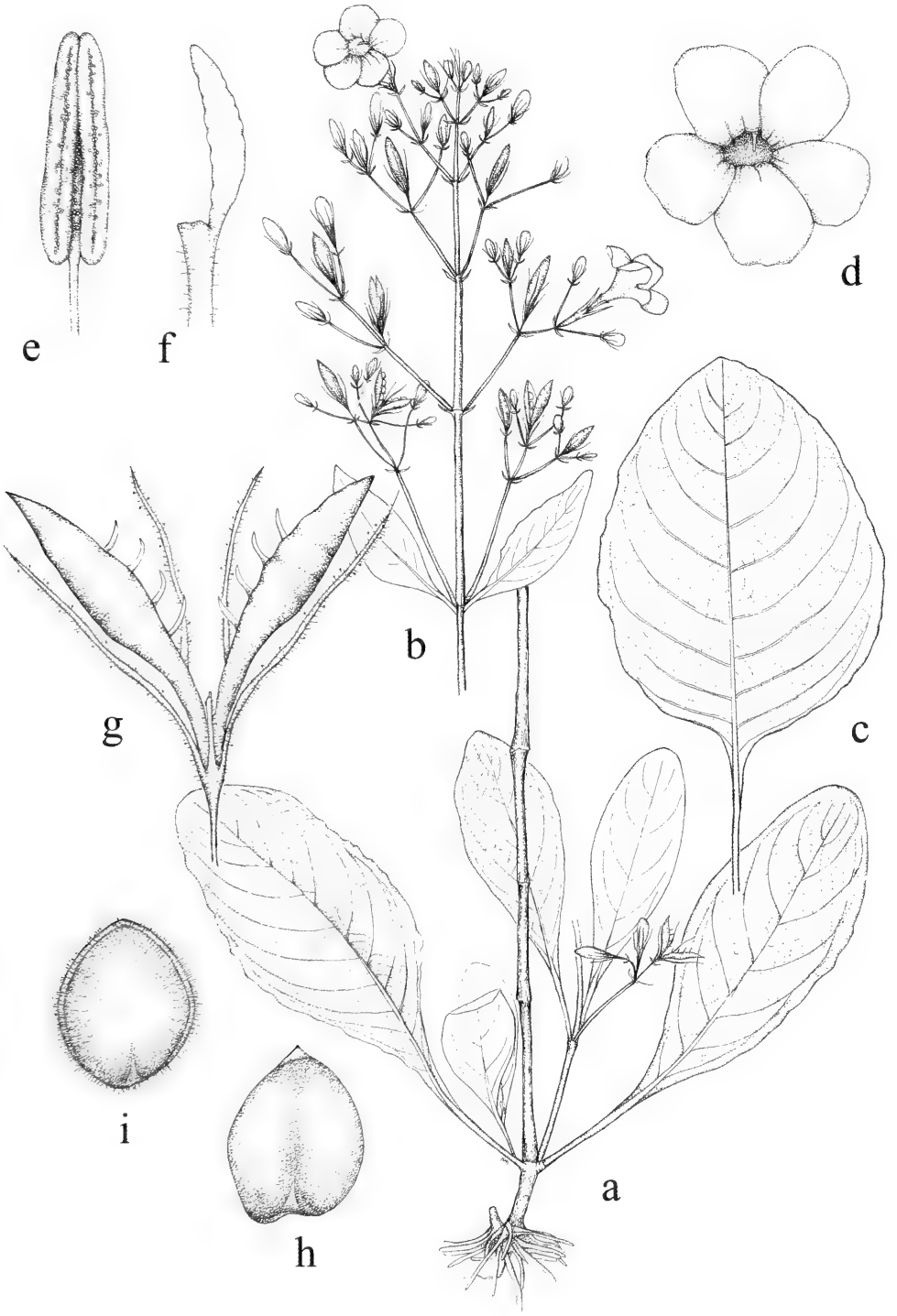
Local names. "Cuetito" (fide White 1949); "papachili" (fide Yetman and Van Devender 2002); "rama del toro" (*Van Devender et al. 95-1074*); "tronador" (fide Yetman and Van Devender 2002).

Use. Yetman and Van Devender (2002) noted that the Mayo use the leaves to brew a tea that is taken to alleviate fever.

Dipteracanthus nudiflorus was based primarily on *Lindheimer 157* from Sims Bayou (the locality does not appear on syntypes at GH or UC, but is noted by Engelmann and Gray in the protologue). In the protologue Engelmann and Gray also cited *Drummond coll. 2, no. 221* (seen at GH and K) and *Drummond coll. 3, no. 257* (seen at GH and K), both from unknown localities in Texas. Leonard (1927) indicated that Lindheimer had collected the type at Sim's Bayou. Because he did not cite a specific specimen, and as there appear to be multiple syntypes, his choice would not appear to constitute a lectotypification. Potential syntypes of *Lindheimer 157* include a specimen at GH with the plant name in Gray's handwriting, a specimen now at GH that came from the Boston Society of Natural History (in whose journal the species was published), and a specimen at UC with the name written apparently by Gray. All of these specimens bear the number "157" which was likely assigned to Lindheimer's plants as they were studied. The three potential syntypes noted above were all collected in 1843 as part of Lindheimer's "fasc. I." Other specimens of this species bearing the number "157" were noted to have been collected by Lindheimer as "fasc. III" in 1846 (e.g., at UC). It is unknown to me whether the specimens of Lindheimer's no. 157 from 1846 were also collected at Sim's Bayou, but because they were collected subsequent to the publication of this name, they would not figure in its typification. To firmly establish a type for this species, a lectotype is here designated for *Dipteracanthus nudiflorus*: *Lindheimer* (*Fasc. I*) *157* (GH-Harvard University Herbaria no. 00093956). The lectotype was collected in 1843 and is mounted on a sheet with a Drummond collection.

Daniel (1995a, 1997, 1999a) and Daniel and Acosta (2003) provided descriptions of this species. Some collections note the presence of white corollas. While it is possible that some plants

FIGURE 34 (right). *Ruellia nudiflora*. a. Habit of base of plant (*Wiggins & Rollins 136*), × 0.49. b. Habit of apex of plant (*Mearns 737*), × 0.43. c. Leaf (*Wiggins & Rollins 136*), × 0.51. d. Corolla (*Daniel & Butterwick 2980*), × 1.3. e. Distal portion of stamen with anther (*Felger et al. 01-459*), × 11.3. f. Distal portion of style with stigma (*Felger et al. 01-459*), × 17.8. g. Capsule with calyx (lobe in front partially removed) (*Mearns 1999*), × 3.1. h. Dry seed (*Daniel & Marrs 1808*), × 6.9. i. Moistened seed (*Daniel & Marrs 1808*), × 6.9. Drawn by Nadia Strasser.


e
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a

may be albinic in corolla color, most collections purporting to have white corollas also indicate that mature flowers were not present or lack them on the specimens. Corolla buds of *R. nudiflora* appear whitish but are invariably blue internally when opened.

This species occurs nearly throughout Sonora (Fig. 35), including occurrences in each subdivision of the Sonoran Desert in the state. Flowering of *Ruellia nudiflora* mostly coincides with the summer rains, but occasional plants have been collected in flower during the spring. Plants are usually found associated with watercourses (i.e., on stream banks, in arroyo bottoms, or in riparian flood zones) or flats or swales where water accumulates following rains.

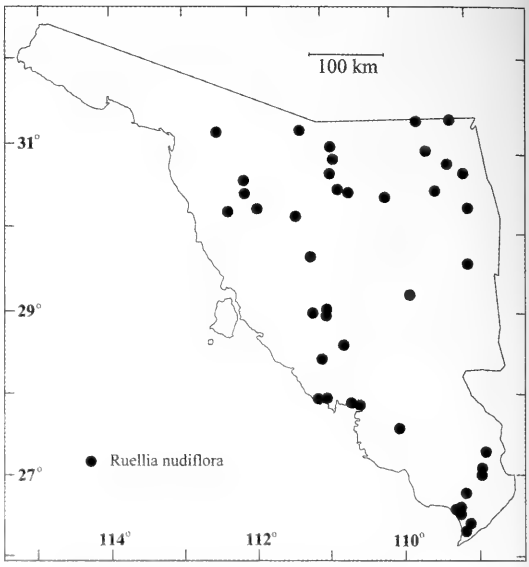

FIGURE 35. Sonoran distribution of *Ruellia nudiflora*.

SONORAN COLLECTION: 2.5 km S de Hermosillo, 29°01′N, 110°57′W, *A. Búrquez & A. Quijada 91-14* (MEXU); from Hwy. 15 to Bahía Agiabampo, ca. 5 km NE of Bahía Agiabampo, ca. lat. 26.41°N, long. 109.20° W, *T. Daniel 9768* (CAS); 4.6 mi N of Fronteras, *R. Felger 4039* (ARIZ, ENCB); 10.2 mi S of La Pintada (between Hermosillo and Guaymas) on Mex. 15, *R. Felger 8364* (ARIZ), *R. Felger & C. Lowe 8364* (ARIZ, MEXU); ca. 7 mi S of Pitiquito, *R. Felger & E. Abbey 20271* (ARIZ); Bahía Algadones, ca. 2 km N of Club Med, *R. Felger & R. Devine 85-333* (ARIZ); 0.8 km E of Las Guásimas, *R. Felger & N. Gonzales 85-382* (ARIZ, MEXU); 9 mi E of Empalme end of Douglas Bridge on Hwy. 15, then 2.5 mi S of Hwy. on Playa del Sol Road, 27°54′N, 110°41′W, *R. Felger & F. Reichenbacher 85-1106* (ARIZ, CAS, MEXU, TEX); road to Bahía San Carlos, 4 mi W of Hwy. 15, *R. Felger & R. Thomas 11941* (ARIZ); SW of Los Camotes on Arroyo Seco, along Los Tanques-Las Chinacas road, 27°16′N, 108°51′W, *M. Fishbein et al. 1880* (ARIZ); Mpio. Magdalena de Kino, Rancho La Tinaja Colorada, ca. 15 km NE de Magdalena de Kino, 30°42′N, 110°48′W, *A. Flores M. et al. 4584* (ARIZ, IEB, MEXU); Mpio. San Pedro de la Cueva, 3 km SW de San José de Batuc, carr. Mazatán–San Pedro de la Cueva, 29°18′N, 109°54′W, A. Flores M. & J. León 5276 (MEXU); Mpio. La Colorada, 2.5 km S de El Pilar, 28°39′N, 110°52′W, *A. Flores M. & J. León G. 5356* (IEB, MEXU); 15 mi S of Hermosillo, *H. Gentry 4562* (ARIZ); Ciénega on the Río Saracahi, 1.7 mi NW of Agua Fria, 30°22′N, 110°35′W, *D. Goldberg 77-126* (ARIZ, MEXU); La Ciénega, *L. Goodding 959* (ARIZ); Logulea [?] to Altar, *D. Griffiths 6895* (MO); vic. of San Pedro, *C. Hartman 955* (MO, UC, US); Nacori Chico drainage, E of Buena, 29°37′N, 108°59′W, E. Joyal 1722 (MEXU); 5.1 mi NW of San Carlos Yacht Club on road to Algadones, *R. Krizman & O. Soule s.n.* (ARIZ); without locality, *E. Palmer 98* (C, MEXU, NY, US); Bacum Station, near Río Yaqui, *F. Pennell 20202* (MEXU, PH, US); 14 mi by Tecolote road W of Mex. 15 (1.4 mi N of El Oasis), 29°48′N, 111°16′W, *F. Reichenbacher 101* (ARIZ); Mpio. Imuris, Agua Caliente, 19 km N of Imuris, 30°57′N, 110°51′W, *A. Reina G. et al. 2001-65* (CAS); Mpio. Agua Prieta, Rancho San Bernardino, 29 km E of Agua Prieta on Mex. 2, 31°20′N, 109°17′W, *A. Reina G. et al. 2003-1005* (CAS); Mpio. Huatabampo, Camahuiroa, 27 km SE of Yavaros, 26°31′N, 109°16′W, *A. Sanders et al. 12713* (CAS); Distr. Altar, Bahio de Aquituni, between Pitiquito and Rancho Verruga, *F. Shreve 6023* (ARIZ); Ejido Manual Caudillo, 7.4 mi S of Luis (ca. 10 mi N of Sinaloa border), *O. Soule & R. Krizman s.n.* (ARIZ); Palm Canyon, SE of Magdalena in Cerro Cinta de Plata, *L. Toolin & T. Van Devender 435* (ARIZ); across Río Bacanuchi from Tauichopa (2.7 mi N of Arispe), *R. Turner & C. Lowe 185* (ARIZ); Alamos, 27°01′N, 108°50′W, *T. Van Devender 94-619* (ARIZ); Ciénega near Rancho Agua Fria on Río Saracachi, E of Cucurpe, *T. Van Devender & C. Miksicek s.n.* (ARIZ, ENCB); Mpio. Sáric, Rancho Los Nogales, Arroyo El Silencio, 19.5 km N of Sáric on old road to Sásabe, 31°15′N, 111°21′W, *T. Van Devender & A. Reina G. 2002-915* (CAS); Mpio. Navojoa, Teachive de Masiaca, Arroyo

Masiaca, 26°47′N, 109°14′W, *T. Van Devender & D. Yetman 94-665* (ARIZ); Mouth of Arroyo Masiaca, Las Bocas on Gulf of California, ca. 52 km S of Navojoa, 26°36′N, 109°20′W, *T. Van Devender & D. Yetman 94-703* (ARIZ); Palm Canyon, 17.7 mi SE of Magdalena in Cerro Cinta de Plata, *T. Van Devender et al. s.n.* (ARIZ); Mpio. Navojoa, Arroyo Masiaca, ca. 0.5 km N of Teachive de Masiaca, 26°48′N, 109°14′W, *T. Van Devender et al. 93-968* (ARIZ, CAS); El Rincon Viejo, ca. 4 km N of Alamos in Sierra de Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 94-654* (ARIZ); 1 km SSW of Sirebampo, 26°37′N, 109°15′W, *T. Van Devender et al. 95-1074* (CAS); 28 mi SE of Guaymas, *U. Waterfall 12830* (TEX, UC, US); 65 mi SE of Sonoita, ca. 31°10′N, 112°20′W, *G. Webster & G. Breckon 15572* (GH, MEXU); near Colonia Oaxaca, Arroyo del Pulpito, *S. White 759* (GH, US); region of the Río de Bavispe, Cañón de las Bellotas, *S. White 3565* (ARIZ, GH, MEXU); 9 mi W of La Angostura, *S. White 4023* (ARIZ, NY, US); Colonia Morelos, *S. White 4111* (ARIZ, NY, US); 7 mi W of Pozo Cerna, *I. Wiggins 6040* (DS); 20 mi W of Norio, *I. Wiggins 6173* (DS, US); along Río de los Alisos, 31 mi S of Nogales, *I. Wiggins 7016* (DS, US); 27 mi W of Hermosillo, *I. Wiggins & R. Rollins 136* (ARIZ, DS, MO, NY, UC, US).

Ruellia parryi A. Gray, Syn. Fl. N. Amer. 2(1):326. 1878. *Dipteracanthus suffruticosus* Torr. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):122. 1859, non *Ruellia suffruticosus* Roxb. (1814). TYPE: MEXICO. Chihuahua: "Presidio del Norte," 7 Jul 1852, *C. Parry* "*722*" (lectotype, designated here, see discussion below: NY [plant at lower right on sheet], photo at http://sidsite.nybg.org/herbim/2970/v-297-00311935big.jpg!).

Erect subshrubs to 6 dm tall. Young stems quadrate-sulcate, internodes glabrous or evenly pubescent with retrorse eglandular trichomes 0.05–0.2 mm long, nodes often with a cluster of flexuose eglandular trichomes to 1.3 mm long. Leaves petiolate, petioles to 8 mm long, blades ovate to lance-elliptic to elliptic to oblanceolate to obovate, 9–25 (–35) mm long, 3–15 mm wide, 1.7–2.8 (–7) times longer than wide, acute to rounded at apex, acute to attenuate at base, surfaces pubescent (sometimes sparsely so) with erect to flexuose (and with at least some branched or stellate) trichomes to 0.8 mm long, margin entire to undulate, usually conspicuously ciliate with trichomes like those of leaf surfaces (or these usually somewhat longer, i.e., to 1.2 mm long). Inflorescence of pedunculate dichasia in leaf axils; dichasia alternate or opposite, 1 per axil, 1 (–3)-flowered, peduncles 0.5–6 mm long, glabrous or pubescent like young stems. Bracteoles subfoliose, petiolate, ovate to lanceolate to elliptic to obovate, 6.5–18 mm long, 2–6.5 mm wide, pubescent like leaves. Flowers sessile. Calyx 5–11 mm long, abaxially pubescent with erect to flexuose (sometimes branched or stellate) eglandular trichomes 0.05–0.2 mm long, tube 1–2 mm long, lobes unequal in size, anterior segment lanceolate to elliptic, 4–9 mm long, 1–1.8 mm wide, apically 2-lobed, lobes ovate to subulate (sometimes asymmetric), 2–7 mm long (sometimes divided nearly to or to the tube), lateral lobes lance-subulate to lanceolate, 2.5–7 mm long, 0.5–0.7 mm wide, posterior lobe lanceolate, 3.5–9 mm long, 0.7–1.2 mm wide, entire. Corolla blue, 20–41 (–50) mm long, externally pubescent with erect to flexuose to retrorse eglandular trichomes 0.05–0.2 mm long, tube 16–38 mm long, narrow proximal portion 8–23 mm long, abruptly expanded distally into throat, throat obconic, 7–13 mm long, shorter than tube or ± equal in length to tube, 2.3–7 mm in diameter near midpoint, limb 12–32 mm in diameter, lobes 5–13 mm long, 5–14 mm wide. Longer stamens 7–9 mm long, shorter stamens 5–6 mm long, thecae 1.8–2 mm long. Style 19–26 mm long, proximally pubescent with eglandular trichomes, distally glabrous; stigma unequally 2-lobed, 1 lobe 0.5 mm long, other lobe 1.2 mm long. Capsule ellipsoid, 9–11 (–13) mm long, (glabrous or) entirely or distally pubescent with retrorse eglandular trichomes 0.1–0.2 mm long. Seeds 6 (or more) per capsule, lenticular, 2.5–3 mm long, 1.9–2.2 mm wide, surfaces and margin pubescent with appressed trichomes.

Phenology. Flowering: August; fruiting: August.

Distribution and habitat. Southwestern United States (Arizona, New Mexico, Texas) and

northern Mexico (Chihuahua, Coahuila, Durango, Nuevo León, Sonora, Zacatecas); Sonoran plants occur on limestone in Chihuahuan desertscrub at an elevation of 1287 m.

Illustrations. *Trees, Shrubs and Woody Vines of the Southwest*, 934. 1960; *Flora of Texas* 1(3):247. 1966; *Trees and Shrubs of Trans-Pecos Texas*, 396. 1988.

In the protologue of *Dipteracanthus suffruticosus*, Torrey cited the following collection data: "Presidio del Norte; July–August; *Parry*. Sides of rocky hills, valley of the Pecos. No. 1461, *Wright*." A lectotype is designated above from among the syntypes in Torrey's protologue. In Torrey's herbarium at NY, there are three pertinent collections: *Wright 1461* from the valley of the Pecos, a collection made by Parry at Presidio del Norte on 7 July 1852 (with "722" also written on the label), and another collection (without the name of the collector) made at Presidio del Norte in August of 1852. The two collections from Presidio del Norte are mounted on the same sheet. Because Torrey referred to unspecified collection(s) by Parry from July and August, he undoubtedly attributed both of these collections to Parry and was including both in his citation of syntypes. Thus there are three syntypes and all of them pertain to what is now treated as *R. parryi*. Tharp and Barkley's (1949) indication of the type as "at Presidio del Norte, *Parry s.n.*" would not appear to constitute lectotypification (either intentional or unintentional) because it does not distinguish between the two syntypes presumably collected by Parry at that locality. The lectotype designated above possesses an open and intact flower (unlike the other syntypes). The type locality, Presidio del Norte, was noted in the protologue to be at the junction of the Río Conchos and Río Grande and is today called Ojinaga.

Ruellia parryi is here reported for the first time from Sonora where it reaches the western extent of its distribution (Fig. 31). It is one of at least three Mexican species of *Ruellia* known to have stellate or dendritic trichomes on mature organs (e.g., leaves, bracteoles, calyx). The other two, *R. hirsutoglandulosa* (Oerst.) Hemsl. and *R. lanatoglandulosa* (Nees) Lindau, occur to the south of the Chihuahuan Desert and differ from *R. parryi* by their longer calyces ((8–) 11–34 mm), usually longer corollas ((32–) 42–85 mm) with the external pubescence including glandular trichomes, and capsular pubescence that includes glandular trichomes. Branched trichomes are sometimes present on the youngest vegetative growth in other Mexican *Ruellia* (e.g., *R. leucantha* Brandegee).

Most plants of *Ruellia parryi*, including those of the sole Sonoran collection, are pubescent more or less throughout. In some (e.g., *Breedlove & Mahoney 71916* from Coahuila) the internodes are glabrous and trichomes on the leaves and bracteoles are largely restricted to the midvein and margin.

Sonoran collection: Mpio. Agua Prieta, NE of Sierra Anibácachi, Rancho La Calera, ca. 10 km SW of Agua Prieta, 31°14′N, 109°38′W, *A. Reina G. et al. 2003-957* (CAS).

Stenandrium Nees

Stenandrium Nees in Lindley, Intr. Nat. Syst. Bot., ed. 2, 444. 1836, nomen cons. TYPE: *Stenandrium mandioccanum* Nees.

Gerardia L., Sp. Pl. 610. 1753, pro parte, nomen rej. vs. *Stenandrium* Nees (1836). LECTOTYPE (Pennell, Bull. Torrey Bot. Club 40:120. 1913): *Gerardia tuberosa* L.

Acaulescent (arising from a woody rhizome or caudex) or caulescent erect to spreading perennial herbs lacking cystoliths. Leaves opposite or quaternate. Inflorescence of axillary or terminal elongate or headlike usually pedunculate dichasiate spikes; dichasia opposite or alternate, 1-flowered, sessile, subtended by a bract. Flowers homostylous, sessile, subtended by 2 homomorphic bracteoles. Calyx deeply 5-lobed, lobes equal or subequal in size. Corolla pink, purple, or white,

tube expanded distally into a short throat, limb 2-labiate or appearing subactinomorphic, upper lip 2-lobed, lower lip 3-lobed, corolla lobes imbricate in bud. Stamens 4, subdidynamous, included in corolla tube, anthers 1-thecous, pubescent, lacking basal appendages, dehiscing toward lower lip (i.e., flower nototribal); pollen (Fig. 18) euprolate to perprolate (to spherical), 3-colpate (rarely inaperturate), exine psilate to foveolate to fossulate to verrucate to gemmate; staminode 0–1, borne between posterior pair of stamens, usually shorter than filaments. Style included in corolla tube, stigma asymmetrically funnelform. Capsule estipitate to substipitate, ellipsoid to obovoid, retinacula present, septa with attached retinacula remaining attached to inner wall of mature capsule. Seeds 4, homomorphic, lenticular, often with barbed or branched trichomes. ($x = 13$).

Stenandrium has traditionally been treated as a New World genus with some 40 to 50 species. Vollesen (1992) included *Stenandriopsis* S. Moore from Africa and Madagascar within *Stenandrium*. Although *Stenandriopsis* in the Old World appears morphologically indistinguishable from *Stenandrium* in the New World, recent molecular studies (McDade et al. 2003) show the former genus to be the basal member of an otherwise New World clade that includes *Stenandrium*. These studies do not support the inclusion of *Stenandriopsis* within *Stenandrium*, but additional research will be necessary to resolve generic boundaries between these and among other genera of tribe Acantheae. Daniel (1985) recognized nine species of *Stenandrium* in Mexico. Concentrations of species are also found in the West Indies (ca. 15 species) and South America (15–25 species).

Stenandrium pilosulum (Blake) T.F. Daniel, Ann. Missouri Bot. Gard. 71:1039. 1984. *Gerardia pilosula* Blake, Contr. Gray Herb. 52:101. 1917. TYPE: MEXICO. Chihuahua: vicinity of Madera, 27 May-3 Jun 1908, *E. Palmer 317* (holotype: GH!; isotypes: MO!, US!).

Acaulescent perennial herbs to 7.5 cm tall from a ± woody caudex or rhizome, the caudex or rhizome bearing numerous fleshy roots along its length. Leaves (plants often leafless or nearly so during anthesis) ascendant, petiolate, petioles to 18 mm long, glabrous or pubescent with a few eglandular trichomes to 0.3 mm long, blades oblanceolate to narrowly elliptic to lanceolate (to ovate), 11–55 mm long, 3–7 (–11) mm wide, 2.8–6.9 (–11) times longer than wide, attenuate to decurrent at base, acute to rounded at apex, surfaces glabrous (although the lower surface inconspicuously glandular along the basal portion) and punctate-pitted, margin red, entire, eciliate. Inflorescence of pedunculate spikes to 30 mm long, peduncles 5–45 mm long, nearly glabrous or pubescent with retrorse to erect trichomes 0.05–0.2 mm long; dichasia opposite to subopposite along spike axis, sessile. Bracts ovate to narrowly elliptic to obovate, 6–12 mm long, 1.5–4.5 mm wide, abaxial surface pubescent like peduncles although with trichomes more numerous, margin inconspicuously ciliate with trichomes 0.05–0.3 mm long. Bracteoles linear to linear-lanceolate, 6–11.5 mm long, 0.5–1.1 mm wide, abaxial surface pubescent like bracts. Calyx 7–14 mm long, lobes linear-subulate to linear-lanceolate, subequal, 6.5–13.5 mm long, pubescent like bracts. Corolla pink with tube and proximal portions of lobes of lower lip white, 10–23 mm long, tube 6–15 mm long, upper lip 3–10 mm long, lower lip 4–10 mm long, lobes subequal, 3–10 mm long, lobes and tube glabrous or sparsely pubescent on external surface, lower-central lobe often densely pubescent on external surface. Stamens 2.5–3 mm long, anthers 1.5 mm long. Capsule 9–12 mm long, pubescent over the entire surface. Seeds 3–4 mm long, 3–3.5 mm wide, densely pubescent with long bristlelike trichomes bearing lateral barbs or branches.

Phenology. Flowering: March–July; fruiting: March.

Distribution and habitats. Sierra Madre Occidental of northwestern Mexico (Chihuahua, Sonora); Sonoran plants occur on gravely slopes, in pastures, and along watercourses in oak-pine communities at elevations from 1540 to 2250 m.

Illustration. Figures 15, 36.

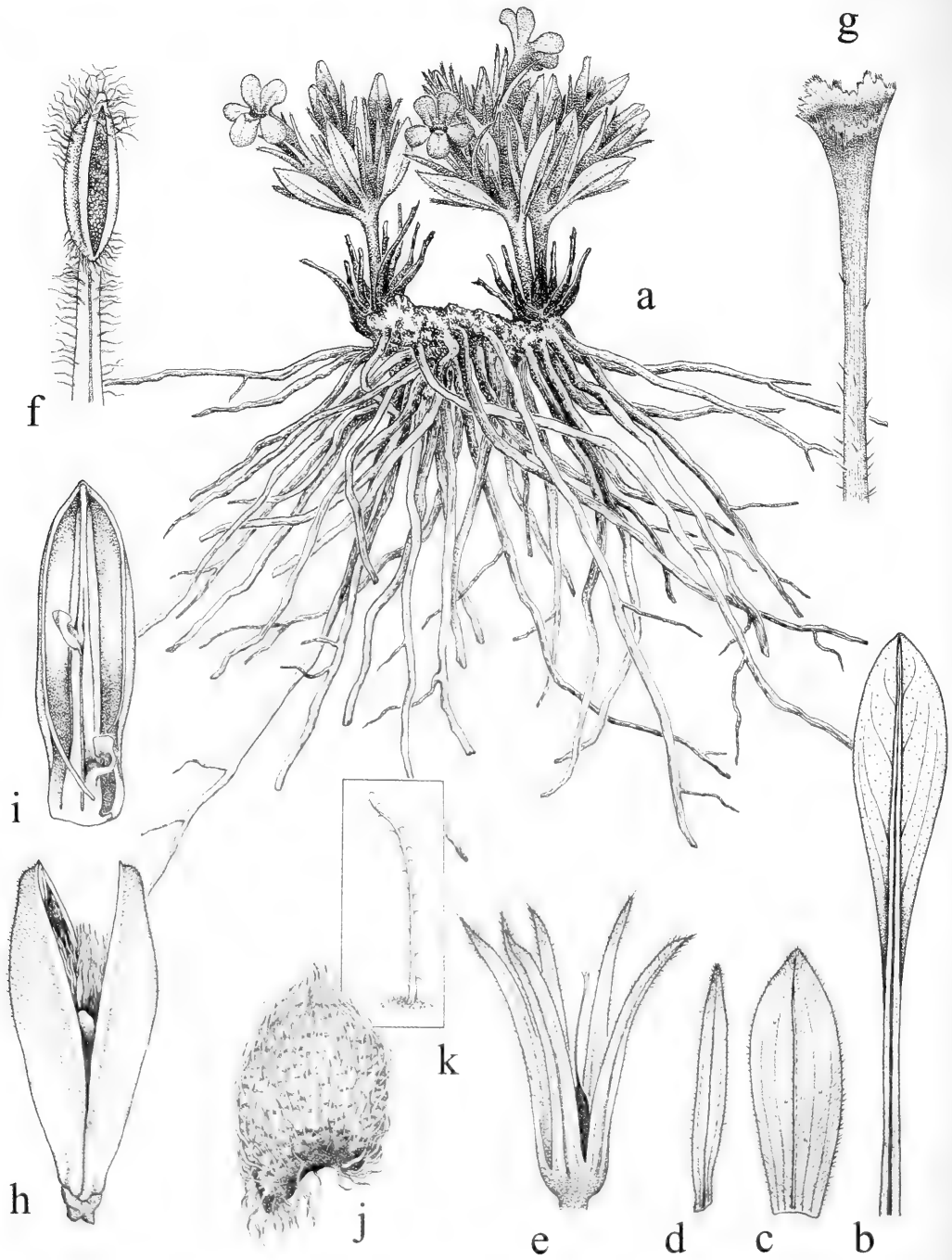

FIGURE 36. *Stenandrium pilosulum*. a. Habit (*Daniel et al. 8614*), × 1. b. Leaf (*Laferriere 439*), × 2. c. Bract (*Daniel et al. 8607*), × 4.3. d. Bracteole (*Daniel et al. 8607*), × 4.3. e. Calyx (*Daniel et al. 8607*), × 3.4. f. Distal portion of stamen with anther (*Daniel et al. 8607*), × 15.8. g. Distal portion of style with stigma (*Daniel et al. 8614*), × 22.7. h. Capsule (*Correll & Johnston 21612*), × 4.4. i. Capsule valve (*Correll & Johnston 21612*), × 4.4. j. Seed (*Correll & Johnston 21612*), × 8.4. k. Trichome from seed (*Correll & Johnston 21612*), × 24. Drawn by Jenny Speckels.

Although Daniel (1985) provided a description of this species, sufficient additional collections from Sonora have become available in the intervening years to warrant an augmented, and more complete one. The species is endemic to the highlands of eastern Sonora (Fig. 37) and western Chihuahua. Corollas are pink with the internal surfaces of the tube and proximal portions of the lobes of the lower lip white. The ventral portion of the tube near its mouth is densely pubescent with yellowish gold trichomes.

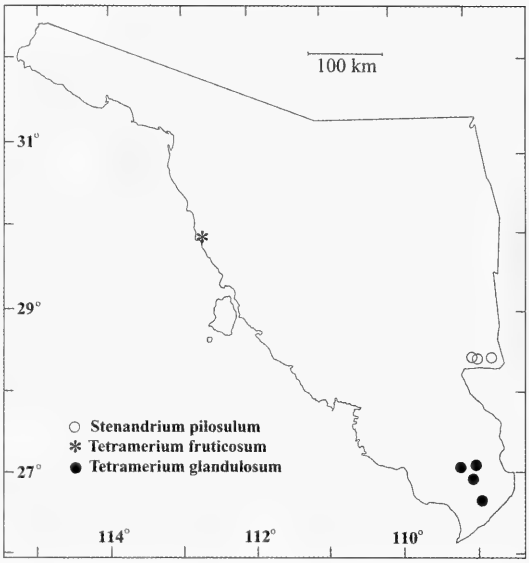

FIGURE 37. Sonoran distributions of *Stenandrium pilosulum, Tetramerium fruticosum*, and *T. glandulosum*.

Sonoran collections: Mpio. Yécora, ca. 0.5 km NW of cemetery in Yécora, ca. 28°23′N, 108°50′W, *T. Daniel et al. 8607* (CAS, MEXU); Mpio. Yécora, El Kípor, 7.4 km E of Maycoba along Hwy. 16, ca. 28°24′N, 108°35′W, *T. Daniel et al. 8614* (CAS, MICH); Rancho La Pinosa, 5.9 mi W of Maycoba on Hwy. 16, 28°25′N, 108°43.5′W, *M. Fishbein et al. 1839* (ARIZ); Yécora, just NW of cemetery, *M. Fishbein et al. 1859* (ARIZ); 28°22.5′N, 108°55.5′W, ca. 5 mi W of Yécora, *P. Hubbell s.n.* (ARIZ); 7 mi NW of Yécora, ca. 28°26′N, 109°00′W, *R. Moran 21965* (CAS, ENCB); Mpio. Yécora, El Kípor (Quipur), Arroyo El Kípor, 28°24′N, 108°36′W, *T. Van Devender & A. Reina G. 95-364* (ARIZ, CAS, MEXU), *97-434* (MO, TEX); Mpio. Yécora, 3–4 km NNW of El Kípor (Quipur), 28°25.5′N, 108°36′W, *T. Van Devender & A. Reina G. 95-405* (ARIZ); ca. 5 mi W of Maicova, 28°22′N, 108°44′W, *G. Webster 23849* (CAS).

Tetramerium Nees

Tetramerium Nees in G. Bentham, Bot. Voy. *Sulphur*, 147. 1846, nom. cons., non C.F. Gaertn. (1806). TYPE: *Tetramerium polystachyum* Nees (= *Tetramerium nervosum* Nees).

Averia Leonard, J. Wash. Acad. Sci. 30:501. 1940. TYPE: *Averia longipes* (Standl.) Leonard (≡ *Drejerella longipes* Standl.; = *Tetramerium nemorum* Brandegee).

Decumbent to erect perennial herbs or shrubs with cystoliths. Leaves opposite (rarely ternate). Inflorescence of terminal conspicuously and usually densely bracteate 4-sided unbranched dichasiate spikes; dichasia opposite, 1–3-flowered, sessile, subtended by a bract. Flowers homostylous, sessile, subtended by 2 homomorphic bracteoles. Calyx deeply 4- or 5-lobed, lobes homomorphic or, if 5, 1 usually ± reduced in size. Corolla white, cream, yellow, blue, or red, often with maroon and purplish markings on upper lip, tube subcylindric or gradually expanded distally, throat indistinct or distinct only near mouth, limb pseudopapilionaceous, upper lip comprising 2 fused lobes, entire to emarginate at apex, lower lip 3-lobed, lower-central lobe (in ours) conduplicate and enclosing stamens and often style during anthesis, corolla lobes imbricate in bud. Stamens 2, exserted from mouth of corolla, anthers 2-thecous, thecae equal to subequal in size, parallel to subsagittate, equally inserted, lacking basal appendages, dehiscing toward upper lip (i.e., flower stenotribal); pollen (Fig. 38) subprolate to perprolate, 3-colporate, 6-pseudocolpate, pseudocolpi 2 per mesocolpium, exine (rugulate to) reticulate to bireticulate; staminodes 0. Style exserted from mouth of corolla, stigma 2-lobed, lobes equal. Capsule stipitate, head ellipsoid to obovoid, retinacula present, septae with attached retinacula slightly separating from inner wall of mature capsule.

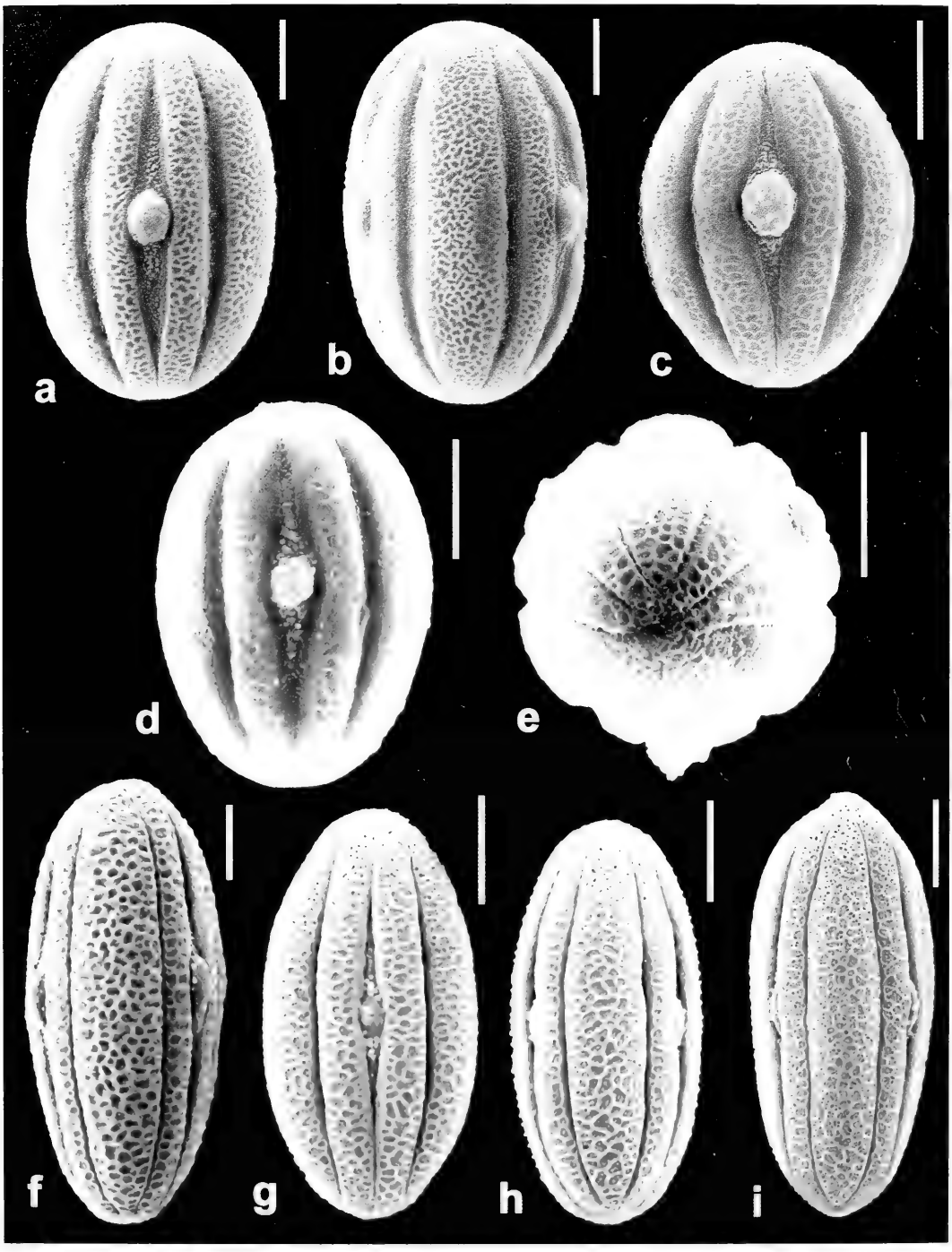

FIGURE 38. Pollen of Sonoran *Tetramerium*. a. *T. abditum* (*Daniel 3364*), apertural view. b. *T. abditum* (*Daniel 3364*), interapertural view. c. *T. fruticosum* (*Daniel & Butterwick 6869*), apertural view. d. *T. nervosum* (*Carter & Moran 5324*), apertural view. e. *T. nervosum* (*Carter & Moran 5324*), polar view. f. *T. glandulosum* (*Van Devender et al. 94-946*), interapertural view. g. *T. tenuissimum* (*Jenkins et al. 88-320*), apertural view. h. *T. tenuissimum* (*Jenkins et al. 88-320*), interapertural view. i. *T. yaquianum* (*Van Devender et al. 92-1109*), interapertural view. Scales = 10 µm.

Seeds 4, homomorphic, plano-convex to concavo-convex), lacking trichomes. ($x = 18$).

This genus of 29 species occurs from the southwestern United States southward throughout most of Mexico, Central America, and northwestern South America to southeastern Bolivia (Daniel 1986). With 22 species, Mexico is the center of diversity of *Tetramerium.*

1. Corollas red to reddish orange, 29–42 mm long, upper lip lacking maroon markings, tube funnelform, 18–25 mm long, 2.8–4.8 mm in diameter at apex; thecae 2.9–3.6 mm long; style 26–37 mm long. ..... *T. abditum*
1. Corollas white, cream, or yellow, 7–26 mm long, upper lip with maroon markings, tube subcylindric, 2.5–9 mm long, 1–2.5 mm in diameter at apex; thecae 0.6–2.6 mm long; style 4–26 mm long.
   2. Viscid shrubs to 3 m tall; herbage conspicuously glandular with glands up to 1 mm long (at least some glands longer than 0.3 mm); corollas bright yellow with 2 maroon stripes on upper lip, 17–26 mm long; thecae 1.7–2.6 mm long; capsules 6–9 mm long. ..... *T. glandulosum*
   2 Perennial herbs to 5 dm tall; herbage eglandular or ± inconspicuously glandular with glands to 0.3 mm long; corollas white, cream, or creamy yellow and with a maroon (and usually purple) chevron on upper lip, 7–17.5 mm long; thecae 0.6–1.5 mm long; capsules 4.5–6.5 mm long.
      3. Calyces 4-lobed; apical portion of bract usually conspicuously twisted. . . . *T. nervosum*
      3. Calyces 5-lobed; apical portion of bract straight (sometimes slightly twisted in *T. yaquianum*).
         4. Capsules glabrous; bracteoles 5–10 mm long. ..... *T. fruticosum*
         4. Capsules pubescent; bracteoles 3–6.5 mm long.
            5. Bracts usually widely spreading (to horizontal or nearly so) from rachis, pubes cence of abaxial surface includes glandular trichomes 0.2–0.3 mm long, margin ciliate with at least some trichomes longer than 0.5 mm; calyx 3.5–4.5 mm long; corolla 13–16 mm long, tube 6-8 mm long. ..... *T. yaquianum*
            5. Bracts erect, closely appressed to rachis, pubescence of abaxial surface includes glandular trichomes 0.05–0.2 mm long, margin ciliate with trichomes to 0.5 mm long; calyx 2–3 mm long; corolla 7-13.5 mm long, tube 2.5–5 mm long. ..... *T. tenuissimum*

Tetramerium abditum (Brandegee) T.F. Daniel, Syst. Bot. Monogr. 12:113. 1986. *Anisacanthus abditus* Brandegee, Zoe 3:348. 1893. TYPE: MEXICO. Sonora: Las Durasnillas, 14 May 1892, *T. Brandegee s.n.* (holotype: UC!; isotypes: F!, GH!).

Phenology. Flowering: November–May; fruiting: November–May.

Distribution and habitats. Western Mexico (Chihuahua, Durango, Michoacán, Nayarit, Sinaloa, and Sonora); Sonoran plants occur on slopes and along watercourses in mesquite scrub, tropical deciduous forests, and oak-pine woodlands at elevations from 230–1360 m.

Illustrations. *The Botany of the Voyage of H.M.S.* Herald, t. 68. 1856; *Systematic Botany Monographs* 12:115. 1986.

Local names. "Rama del toro" (fide Yetman and Van Devender 2002); "viipsumar u'us" (Pima Bajo, *Rea 1069*).

Daniel (1986) provided a description of this species and discussed (2004b) its distribution and distinctions from the morphologically similar *T. rubrum* Happ. *Tetramerium abditum* attains the

northern extent of its distribution in east-central Sonora (Fig. 39). The location of the type locality is discussed above under *Henrya*.

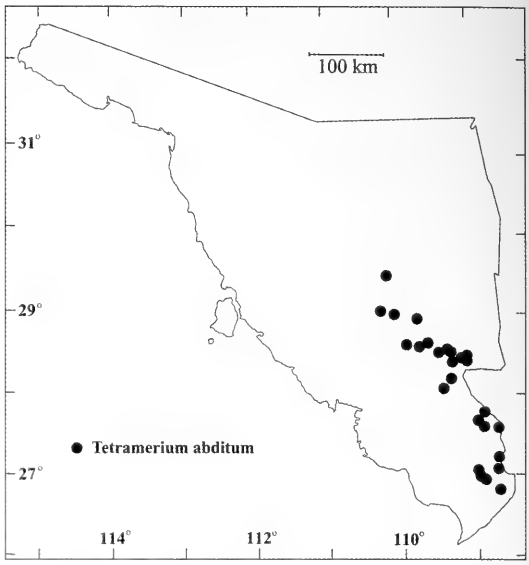

FIGURE 39. Sonoran distribution of *Tetramerium abditum*.

SONORAN COLLECTIONS: San Javier, microondas en el Cerro El Durazno, 28°37′N, 109°45′W, *A. Búrquez 94-019[a]* (MEXU); Cerro El Verde, San Javier, 28°33–34′N, 109°43–44′W, *A. Búrquez et al. 96-066* (MEXU), *96-088* (MEXU); Mpio. Yécora, Santa Rosa, 28°28′N, 109°06′W, *A. Búrquez M. 96-228* (CAS); between Hwy. 16 E of Tonichi and Onavas, 0.5 mi S jct. Hwy. 16, *T. Daniel 3347* (ASU, CAS, MEXU); between Rosario de Tezopaco and Nuri, 7.1 mi S of turnoff to Nuri, *T. Daniel 3364* (ASU, CAS, ENCB, MEXU, MICH, MO, NY, US); Río Cuchujaqui, 7.4 mi SE of Alamos toward Guiricoba, *T. Daniel 3378* (CAS), *T. Daniel 3998* (CAS); Mpio. Yécora, between San Nicolás and Nuri, ca. 6.4 km SW jct. Hwy. 16, ca. 28°24′N, 109°14′W, *T. Daniel et al. 8570* (BR, CAS, K, MEXU, MO); Sierra de Alamos, Arroyo Uvalama (Igualamas), 27°01′N, 108°59′W, *M. Fishbein et al. 1095* (ARIZ, CAS); Arroyo Guajaráy, upstream from village of Guajaráy, 27°37′N, 108°57′W, *M. Fishbein et al. 1553* (ARIZ, CAS); 21.5 mi E of Tecoripa, *P. Gallagher et al. 287* (ASU); Distr. Alamos, Agua Caliente, *H. Gentry 898* (ARIZ, DS, MICH); Caramechi, Río Mayo, *H. Gentry 1178* (A, ARIZ, F, K, MEXU, MICH, MO, NY, UC, US); vicinity of Alamos, *H. Gentry 4801* (ARIZ, DS, GH, MEXU, MICH, MO, NY, UC); 5 mi W of El Novillo Dam, *D. Goldberg 76-66* (ARIZ); 10 mi W of Nuri, *D. Goldberg s.n.* (ARIZ); W of Piedras Verdes near Mocuzari Reservoir, 15 km NW of Alamos, *P. Jenkins 89-127-A* (ARIZ); Naranjo, 27°14′N, 108°43′W, *P. Jenkins 89-316* (ARIZ); Mpio. Alamos, Arroyo Verde, 27°06′N, 108°43′W, *P. Jenkins 90-313* (ARIZ); Hwy. 16 E of Onavas turn-off, 28°35′N, 109°30′W, *E. Joyal 1674* (CAS, MEXU); Río Cuchujaqui, cave next to Mesa Redonda, 27°05′N, 108°45′W, *P. Martin & G. Ferguson s.n.* (ARIZ, CAS); Mpio. Alamos, 3.5 mi SW of Rancho Santa Barbara, 27°06′N, 108°45′W, *P. Martin & G. Ferguson s.n.* (ARIZ); 6 mi NNW of Alamos, *P. Martin & M. O'Rourke s.n.* (ARIZ); cajón of Cuchujaqui, 27°03', 108°44′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); above Las Animas, 27°31.5′N, 108°42′W, *P. Martin et al. s.n.* (ARIZ); El Reparo near Santa Ana de Yécora, *G. Monson s.n.* (ARIZ); near Onavas, 15–20 km NE along Hwy. 16, *A. Rea 1069* (ARIZ); 4 km W of Agua Amarilla, 18.9 km NNW of Tepoca on Mex. 16, 28°29′N, 109°22′W, *A. Reina G. & T. Van Devender 97-371* (ARIZ, CAS, MEXU, TEX); Arroyo El Mentidero at El Chinal road, 11.3 km S of Alamos, 26°55′N, 108°55′W, *A. Reina G. et al. 98-24* (ARIZ); Mpio. Onavas, 4.3 km SE of Onavas junction on Mex. 16, 28°31′N, 109°28′W, *A. Reina G. et al. 2001-155* (ARIZ, MO); Hwy. 16, ca. 8 km E of Tecoripa, Rancho San Juanico, *R. Rondeau 89-82* (ARIZ); Cerro Redondo, 27°05′N, 108°45′W, *R. Rondeau & G. Rodda s.n.* (ARIZ); ca. 5 mi below Minas Nuevas, *J. Rose et al. 12669* (US); vicinity of Alamos, *J. Rose et al. s.n.* (F, GH); Mpio. Mazatán, Sierra de Mazatán, Cañada El Carrizo, N de Rancho El Carrizo, 29°03′N, 110°12′W, *J. Sánchez E. et al. 04-045* (CAS); Mpio. Alamos, Cañón Algoroba, Sierra de Alamos, ca. 27°00′N, 108°57′W, *A. Sanders & L. Lubinsky 13452* (TEX); lower crossing of Río Cuchujaqui, 8 mi SE of Alamos, ca. 26°56′N, 108°53′W, *A. Sanders et al. 2636* (CAS, TEX); 2.2 mi E of San Nicolás, ca. 8 mi NE of Curea, *A. Sanders et al. 2679* (ASU); vicinity of Alamos, *E. Smith 3960* (CAS, MEXU, TEX); 18.5 mi SE of Río Yaqui crossing at Mex. 16, *G. Starr & C. Starr 184* (ARIZ), *Starr et al. 44* (ARIZ); Mpio. Alamos, Sierra de Alamos, Arroyo El Huirotal, ca. 26°57.5′N, 108°57.5′W, *V. Steinmann 95-04* (ARIZ, MEXU); above El Novillo, 83 mi E of Hermosillo, *L. Toolin & K. Roever 576* (ARIZ); 4 mi S of Mazocahui, *R. Turner et al. 59-72* (ARIZ, CAS, UC); 12 mi S of Soyopa, *R. Turner et al. 71-89* (ARIZ, UC); Arroyo Hondo, 10 mi N of Nuri, *R. Turner et al. 75-33* (ARIZ, SD, UC); Río Cuchujaqui at Rancho El Conejo, 12.4 km S of Alamos, 26°55′N, 108°55′W, *T. Van Devender 92-563* (ARIZ); crossing of Río Cuchujaqui on road to Guirocoba, ca. 8 mi SE of Alamos, *T. Van Devender et al. 84-144*

(ARIZ); SE slopes of Sierra de Alamos, Arroyo El Mentidero, Rancho Uvalama, 11 km WSW of Alamos, 26°55′N, 108°55′W, *T. Van Devender et al. 92-53* (CAS); El Guayabo crossing of Río Cuchujaqui, 1.1 mi NE of Sabinito Sur, 14 km ESE of Alamos, 27°00′N, 108°48′W, *T. Van Devender et al. 92-228* (ARIZ, CAS); Río Cuchujaqui at Rancho El Conejo, 13.4 km S of Alamos, 26°54′N, 108°55′W, *T. Van Devender et al. 92-615* (ARIZ); Arroyo El Mentidero at crossing of El Chinal road, 11.5 km S of Alamos, 26°55′N, 108°55′W, *T. Van Devender et al. 93-73* (ARIZ, CAS); below Guajaray on Arroyo Guajaray, 6.5 km WNW of jct. with Río Mayo, 27°36′N, 108°56′W, *T. Van Devender et al. 93-464* (ARIZ); canyon N of Los Aguaros on Arroyo Guajaray, 27°38.5′N, 108°58′W, *T. Van Devender et al. 93-490* (ARIZ, in part); Mpio. Yécora, Agua Amarilla (Los Pinitos), 15 km WNW of Tepoca, 24.7 km WNW of San Nicolas on Mex. 16, ca. 28°08′N, 109°20′W, *T. Van Devender et al. 96-25* (ARIZ, CAS); San Javier, Arroyo San Javier, 1 km S del poblado y 1.5 km N del Cerro El Verde, 28°35′N, 109°44′W, *L. Varela E. 96-51* (MEXU); N side of Sierra de Alamos, *S. Walker 73H34* (DES); Rancho La Sierrita, E slopes of Sierra de Alamos, ca. 6 km SSW of Alamos, 26°58′N, 108°57′W, *J. Weins et al. 93-027* (ARIZ).

Tetramerium fruticosum Brandegee, Zoe 5:171. 1903. TYPE: MEXICO. Baja California Sur: San José del Cabo, Jan-Mar 1901, *C. Purpus 489* (holotype: UC!; isotypes: CAS!, GH!, MO!, NY!, US!).

Phenology. Flowering: October; fruiting: October.

Distribution and habitats. Northwestern Mexico (Baja California Sur, Sonora); Sonoran plants occur in Sonoran desertscrub (Central Gulf Coast) at an elevation between 500 and 600 m.

Illustration. *Proceedings of the California Academy of Sciences* 49:399. 1997.

Daniel (1986, 1997) provided descriptions of this species. *Tetramerium fruticosum* is widespread in Baja California Sur, but known from the Mexican mainland only by a single collection (Fig. 37) from the Central Gulf Coast subdivision of the Sonoran Desert near Puerto Libertad (i.e., the northern extent of its geographic range). Daniel (1986) discussed its distribution in some detail.

Sonoran collection: Tinaja Picu in Picu Mts., 2 mi N of concrete monument set on N side of Libertad Road, *I. Wiggins 6055* (DS).

Tetramerium glandulosum Oerst., Vidensk. Meddel. Dansk Naturhist. Foren. Kjøbenhavn 1854:171. 1854. TYPE: MEXICO. Oaxaca: Río de las Vueltas, Dec 1842, *Liebmann 10751* (holotype: C!).

Tetramerium aureum Rose, Contr. U.S. Natl. Herb. 1:349. 1895. *Justicia aurea* (Rose) Lindau, Bull. Herb. Boissier 5:675. 1897. TYPE: MEXICO. Colima: without specific locality, 9 Jan-6 Feb 1891, *E. Palmer 1302* (holotype: US!; isotypes: GH!, K!, NY!, US!).

Cardiacanthus fragrans Lindau, Bull. Herb. Boissier 7:577. 1899. TYPE: MEXICO. Oaxaca: Distr. Nochixtlán, El Parián, 15 Dec 1895, *C. Seler & E. Seler 1565* (holotype: B, destroyed; lectotype, designated by Daniel, 1986: K!; isolectotypes: A!, CAS!, GH!, MEXU!, NY!, POM!).

Anisacanthus stramineus Barneby, Rhodora 72:70. 1970. TYPE: MEXICO. Puebla: near Coxcatlán, 18 Nov 1966, *H. Ripley 14731* (holotype: NY!; isotype: US!).

Phenology. Flowering: April, December; fruiting: April, December.

Distribution and habitats. Western and southern Mexico (Chihuahua, Colima, Durango, Guerrero, Jalisco, Michoacán, Morelos, Oaxaca, Puebla, Sinaloa, and Sonora); Sonoran plants occur along watercourses in tropical deciduous forests at elevations from 350 to 400 m.

Illustrations. Figure 9; *Systematic Botany Monographs* 12:64. 1986.

Daniel (1986) provided a description of this species, which attains the northern and western extents of its distribution in southern Sonora (Fig. 37).

Sonoran collections: La Calera, 5.5 km N of Alamos Hwy. at El Carrizal, 27°07′N, 109°01.5′W,

P. Martin & M. O'Rourke s.n. (ARIZ); 23 km E of Navojoa, *R. Moran 4033* (DS, SD, US); Mpio. Alamos, Arroyo Las Rastras, SW edge of Sierra de Alamos, 26°57′N, 109°03′W, *T. Van Devender et al. 93-1457* (ARIZ, CAS); Cerro Huacharibi, 4 km SW of Basiroa, 26°41′N, 108°55′W, *T. Van Devender et al. 94-946* (ARIZ, CAS).

Tetramerium nervosum Nees in G. Bentham, Bot. Voy. *Sulphur*, 148. 1846. TYPE: ECUADOR. Guayas: Puna, 1836-1839, *A. Sinclair s.n.* (holotype: K!).

Tetramerium hispidum Nees in A. de Candolle, Prodr. 11:468. 1847. TYPE: MEXICO. Hidalgo: prope las Ajuntas ad flumen Montezuma, Jan, *C. Ehrenberg 1072* (lectotype, designated by Happ, 1937: B, destroyed; isolectotypes: GH!, PR!; probable isolectotype: P!).

Tetramerium nervosum var. *hispidum* Torr. in W.H. Emory, Rep. U.S. Mex. Bound. 2(1):125. 1859. TYPE: MEXICO. Sonora: Santa Cruz, Sep 1851, *G. Thurber 918* (lectotype, designated by Daniel, 1986: NY!; isolectotypes: F!, GH!, NY!).

Dianthera sonorae S. Watson, Proc. Amer. Acad. Arts 24:67. 1889. TYPE: MEXICO. Sonora: vicinity of Guaymas, Sep 1887, *E. Palmer 240* (holotype: GH!; isotypes: C!, K!, NY, US!).

Tetramerium scabrum Happ, Ann. Missouri Bot. Gard. 24:532. 1937. TYPE: MEXICO. Sonora: Fronteras, Jun 1851, *G. Thurber 432* (holotype: NY!; isotypes: CAS!, GH!).

See Daniel (1995a) for a complete listing of synonyms for this species.

Phenology. Flowering: throughout the year, with peaks in March and October (Fig. 1); fruiting: throughout the year.

Distribution and habitats. Southwestern United States (Arizona, New Mexico, Texas), Mexico (Baja California Sur, Campeche, Chiapas, Chihuahua, Coahuila, Colima, Durango, Guanajuato, Guerrero, Hidalgo, Jalisco, México, Michoacán, Morelos, Nayarit, Nuevo León, Oaxaca, Puebla, Querétaro, San Luis Potosí, Sinaloa, Sonora, Tamaulipas, Veracruz, Yucatán, Zacatecas), Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Colombia, Venezuela, Ecuador, and Peru; Sonoran plants occur on slopes, along watercourses, and in disturbed areas in Sonoran desertscrub (Arizona Upland, Central Gulf Coast), palm oases, thornscrub, tropical deciduous forests, grasslands, oak woodlands, and oak-pine woodlands at elevations from 20 to 1450 m.

Illustrations. *Botany of the Voyage of H.M.S.* Sulphur, t. 48. 1845; *Acta Botanica Venezuelica* 8:165. 1973; *Fieldiana, Botany* 24 (10):455. 1974; *Flora of Baja California*, 196. 1980; *Systematic Botany Monographs* 12:58. 1986; *Flora of Chiapas* 4:146. 1995; *Flora del Valle de Tehuacán-Cuicatlán* 23:88. 1999.

Local names. "Abahaca del monte" (*Reina G. et al. 2001-653*); "cola de víbora" (Yetman 2002); "tapa chorro" (*Mexican, Rea 1260*); "saya huehuásira" (Guarijío, Yetman 2002); "tapachorro" (*Varela E. 96-309, 96-456*); "tóskonig" (Pima Bajo, *Rea 1260*).

Uses. Remedy for diarrhea (*Rea 1260*; *Varela E. 96-309, 96-456*); treatment for stomach ache (*Reina G. et al. 2001-653*).

Descriptions of this widespread and morphologically variable species were provided by Daniel (1986, 1995a, 1997, 1999a) and Daniel and Acosta (2003). The morphological diversity throughout its range was discussed in detail by Daniel (1986). Sonoran plants exhibit both white and yellow corollas and have 4-calyx lobes (see Daniel 1986 for discussion of the variation in calyx lobe number in *T. nervosum*). The species is widespread throughout the eastern half of Sonora (Fig. 40), but is largely absent from the drier western half. Indeed, its occurrences in the Sonoran Desert are very rare and may be restricted to riparian sites. In northern Sonora, the species is especially common in desert grasslands and in southern Sonora it is abundant in both thornscrub and tropical deciduous forests.

One collection from Sonora (*Van Devender & Reina G. 2001-184*) that resembles *T. nervosum*

by its relatively long (to 1.5 mm) trichomes on the bracteal margins and lack of glandular trichomes in the inflorescence differs from that species by its five calyx lobes, ± antrorse (vs. straight) trichomes on the bracteal margins, and by the generally flat and straight apical portions of the bracts. Whether it represents a hybrid (e.g., between *T. nervosum* and *T. tenuissimum*), an undetected species, or an unusual form of *T. nervosum* remains undetermined. *Tetramerium nervosum* and *T. tenuissimum* sometimes grow within several centimeters of one another (e.g., *Daniel et al. 8636* and *8637*), but no evidence of hybridization was noted within this or other Sonoran populations of the species. Daniel (1986) discussed the results of attempted artificial crosses between these and between these and other species of the genus.

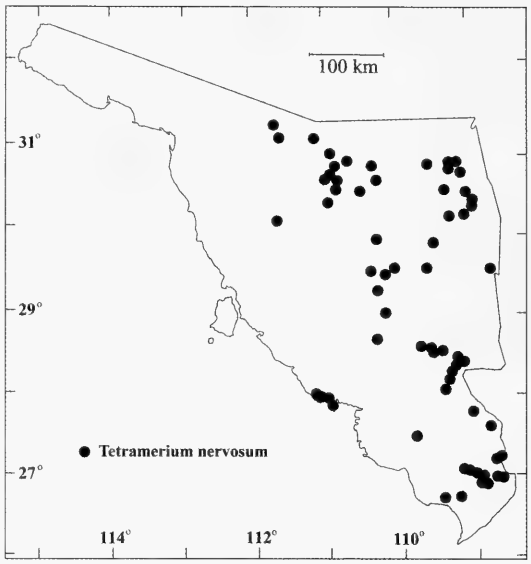

FIGURE 40. Sonoran distribution of *Tetramerium nervosum*.

SONORAN COLLECTIONS: near Guaymas, *L. Bailey 267* (F); Agua María, along Hwy. 16 at KM 200 W of Tepoca, ca. 28°17.5′N, 109°20′W, *G. Boyer et al. s.n.* (ARIZ); 8 km NW of Trigo on road from Yécora to Suarahipo, *D. Breedlove 61074* (CAS, MEXU, MO); near Magdalena, *C. Carter s.n.* (MICH); San Pedro Bay, *T. Craig 680* (POM); between Cananea and Arizpe, 27.7 mi N crossing of Río Bacanuchi, ca. 30°50′N, 110°20′W, *T. Daniel 921* (CAS, ENCB, MEXU, MICH); between Cananea and Arizpe, 16.1 mi S of Río Bacanuchi, *T. Daniel 927* (MICH); between Hermosillo and Sahuaripa, 3 mi W of Mazatán, *T. Daniel 953* (MICH); between Navojoa and Alamos, 24.6 mi E jct. Hwy. 15 in Navojoa, *T. Daniel 1000* (CAS, MICH); Nacapuli Canyon, ca. 4.4 mi N of San Carlos, *T. Daniel 1968* (ASU); along Hwy. 16 between Tecoripa and Tonichi, 13.4 mi W of Río Yaqui, *T. Daniel 3343* (CAS); between Hwy. 16 E of Tonichi and Onavas, 0.5 mi S jct. Hwy. 16, *T. Daniel 3349* (ASU, CAS); between Rosario de Tezopaco and Nuri, 8.1 mi S of turn to Nuri, *T. Daniel 3362* (ASU); Sierra Bojihuacame E of Cd. Obregón, 1.2–2.2 mi SE of Bachoco, *T. Daniel 3369* (CAS); road to El Tezal, 0.2 mi N of hwy. between Navojoa and Alamos, 2.6 mi W of Alamos, *T. Daniel 3375* (ASU), *3385* (ASU, CAS, ENCB, MICH, NY); Río Cuchujaqui, 7.4 mi SE of Alamos toward Guiricoba, *T. Daniel 3380* (ASU, CAS, MEXU, NY, US), *3989* (CAS); 0.2 mi N of Navajoa–Alamos hwy. toward El Tezal, 2.6 mi W of Alamos, *T. Daniel 3385* (CAS, MEXU); southeastern border of Alamos (road to mirador), ca. lat. 27°01′N, long. 108°56′W, *T. Daniel 9772* (CAS); Río Cuchujaqui, ca. 8 mi SE of Alamos, *T. Daniel & M. Butterwick 3193* (CAS, MEXU); Mpio. Yécora, between San Nicolás and Nurí, just S of Curea, ca. 24 km SW jct. Hwy. 16, ca. 28°19′N, 109°17′W, *T. Daniel et al. 8573* (CAS); Mpio. Yécora, Arroyo La Quema, 0.3 km SE of Tepoca on Hwy. 16, ca. 28°26′N, 109°15′W, *T. Daniel et al. 8636* (BR, CAS, K, MEXU, MICH); mountain W of Alamos, *F. Drouet & D. Richards 3956* (F); 20 mi NE of Ures, *F. Drouet et al. 3598* (F); ca. 5 km W of Pilares de Nacozari, *F. Drouet et al. 3672* (F); 21 mi SE of Ures, *F. Drouet et al. 3729* (F); Rancho la Brisca, 3.5 mi N of Agua Fria, 30°24′N, 110°33′W, *J. Duek s.n.* (ARIZ); 35.6 mi NE of Nuri, *D. Dunn 9064* (RSA); Hwy. 2, Imuris, *J. Dwyer 14131* (CAS, MO); ca. 1 km N of Bahía San Carlos on old road to Bahía Algadones, *R. Felger & R. Devine 85-330C* (ARIZ), *R. Felger et al. 84-193* (ARIZ, MEXU); Arroyo Nacapules, ca. 0.5–0.8 km E of mouth of Cañón Nacapules, 6 km N of Bahía San Carlos Road, 28°00′N, 111°02′W, R. *Felger & F. Reichenbacher 85-1178* (ARIZ, CAS, TEX); Cañón Nacapuli, 4.7 mi N of San Carlos Road, 28°00′N, 111°02–03′W, *R. Felger & F. Reichenbacher 85-1222* (ARIZ, CAS, MO, TEX), *R. Felger & R. Thomas 11862* (ARIZ, CAS, MEXU); ca. 1 mi N of Bahía San Carlos toward Bahía Algadones, *R. Felger & A. Russell 9598* (ARIZ, CAS, MEXU); El Baviso, ca. 2.5 km NE of Bahía San Carlos, *R. Felger & D. Valdez Z. 84-517* (ARIZ); Sierra el Aguaje, Cañón las Barajitas, ca. 18 km NW of San Carlos, ca. 28°03′N, 111°10′W, *R. Felger*

& M. Wilson 95-237 (ARIZ, CAS, MEXU); Mpio. Guaymas, Cañón La Balandrona N side of Sierra El Aguaje, 28°06′N, 111°04′W, *R. Felger et al. 01-719* (CAS); 4.1 mi E of Alamos, *J. Fish 158* (UC); Las Camotes, 6 mi NE of Los Tanques, 27°17′N, 108°50′W, *M. Fishbein et al. 80* (ARIZ); Conejos, Río Mayo, *H. Gentry 1121A* (F); Alamos, Río Fuerte, *H. Gentry 2926* (ARIZ, GH, MEXU, MO, S); KM 75 on Hwy. 15, N of Guaymas, *A. Gibson & L. Gibson 2028* (RSA); 4.3 km SW of Santa Ana de Yécora on road to Nuri, 28°23′N, 109°19′W, *D. Goldberg & S. McLaughlin 77-183* (ARIZ); Cohuto, *C. Hartman 76* (F, GH, PH, UC, US); 4 mi N of Colonia Oaxaca, *J. Hastings & R. Turner 65-28* (ARIZ, DS, SD); 16 mi E of Moctezuma, *J. Hastings & R. Turner 65-101* (ARIZ, DS, SD); Río El Naranjo crossing N of Taymuco, 27°15′N, 108°43′W, *P. Jenkins & P. Martin 88-174* (ARIZ); 20 km W of Alamos, 27°07′N, 109°10′W, *P. Jenkins et al. 88-65* (ARIZ); San Carlos Bay, *I. Johnston 4362* (CAS, GH, UC); Las Cabras, ESE of Alamos, 26°50′N, 108°55′W, *E. Joyal 1422A* (CAS); Rancho El Aguilar Noria, N of Ures, 29°33′N, 110°25–26′W, *E. Joyal 1817* (MEXU, TEX); 72 mi E of Hermosillo, *E. Lehto et al. L19299* (ASU); El Guayabo along Río Cuchujaqui, 27°00′N, 108°47′W, *P. Martin s.n.* (ARIZ); 8 km E of Alamos on road to Sabinito Sur, *P. Martin s.n.* (ARIZ); 16 km SE of Alamos, *P. Martin s.n.* (ARIZ); Río Santo Domingo (2 km N of Rancho La Brisca), 30°25.5′N, 110°33′W, *P. Martin s.n.* (ARIZ); 1 km NE of Bachoco, 26°44′N, 109°21′W, *P. Martin & M. O'Rourke s.n.* (ARIZ); Las Chinacas and vicinity of road to Chinipas, 27°14′N, 108°39′W, *P. Martin et al. s.n.* (ARIZ); "Agua Amarilla," ca, 28°27′N, 109°20′W, *P. Martin et al. s.n.* (TEX); Canyon de las Palmas, Sierra Baviso, 16 mi SE of Magdalena, *N. McCarten 2300* (ENCB); Rte. 15, 18.7 mi N of Imuris, *L. McGill & D. Pinkava 6595* (ASU); Mpio. Guaymas, 3 km NE del Aguaje de Robinson, Cañón Los Anegados, 28°02′N, 111°10′W, *L. Moreno et al. 16* (ARIZ); Mpio. Nacore Chico, El Río Bonito near La Nopalera, *C. Muller 3683* (GH, LL, UC, US); Magdalena, *C. Orcutt 1922:1352* (US); Nacopuli Canyon, N of San Carlos, *B. Perrill 5658* (ARIZ); Valle de Teras (just E of La Angostura), *E. Phillips 761* (MICH); Horconcitas, *E. Phillips 837* (MICH); between Horconcitos and Bacerac, *E. Phillips 852* (GH, MICH); near Onavas, *A. Rea 491* (ARIZ); Onavas graphite mine, ca. 28°28′N, 109°32′W, *A. Rea 1260* (ARIZ); northern Sierra Aconchi, 7 mi W of San Felipe, 29°52′N, 110°21′W, *F. Reichenbacher 1172* (ARIZ); Mpio. Santa Ana, Arroyo El Papago, 13 km ENE of Benjamin Hill, 30°16′N, 110°52′W, *A. Reina G. & E. Reina G. 97-1609* (CAS); Mpio. Yécora, base of Cerro El Pilar, above Arroyo Santa Ana, 5.5 km N of Curea on Son. 12, 28°20′N, 109°15′W, *A. Reina G. et al. 99-803* (CAS); Mpio. Guaymas, old road to Algodones, San Carlos, 27°58′N, 111°04′W, *A. Reina G. & T. Van Devender 2000-915* (CAS); Mpio. Yécora, 1.5 km SW of Santa Ana on road to Guadalupe Tayopa, 28°23′N, 109°09.5′W, *A. Reina G. et al. 96-521* (ARIZ); Mpio. Imuris, Agua Caliente, 19 km N of Imuris, 30°57′N, 110°51′W, *A. Reina G. et al. 2001-653* (CAS); ca. 5 mi below Minas Nuevas, *J. Rose et al. 12672* (NY, US); vicinity of Alamos, *J. Rose et al. 12741* (NY, US); vicinity of Puerta de Mano, 26°59′N, 108°39′W, *J. Salmon s.n.* (ARIZ); 5–7 mi E of Alamos toward upper crossing of Río Cuchujaqui, ca. 26°59′N, 108°50′W, *A. Sanders et al. 8833* (CAS); Mpio. Villa Pesqueira, Sierra Pinta, ca. 33 mi S of Moctezuma, ca. 29°35′N, 110°01′W, *J. Shortman & M. Wilson 96-65* (ARIZ); Distr. of Altar, near Los Molinos, *F. Shreve 6014* (F); 10 mi SE of Magdalena, *F. Shreve 6628* (ARIZ, F, GH, MICH, MO); Cerro las Campas, 2.6 mi ESE of Alamos on road to Río Cuchujaqui crossing near Sabinito Sur, 27°01′N, 108°54′W, *G. Starr & D. Palzkill 329* (ARIZ); 7.5 mi W of Alamos, road to Navojoa, *G. Starr & C. Starr 242* (ARIZ); Mpio. Imuris, microondas 14 km S de Imuris, 30°52′N, 110°50′W, *P. Tenorio L. & C. Romero de T. 13495* (CAS); Mpio. Yécora, La Concepción, 29°19′N, 109°02′W, *W. Trauba s.n.* (CAS); Guirocoba crossing of Río Cuchujaqui, 12.3 km SSE of Alamos, 26°56′N, 108°53′W, *T. Van Devender 92-532* (ARIZ); Río Cuchujaqui at Rancho el Conejo, 12.4 km S of Alamos, 26°55′N, 108°55′W, *T. Van Devender 92-564* (ARIZ); 59 km ESE of Hermosillo on Sonora 16, *T. Van Devender & V. Markgraf s.n.* (ARIZ); Mpio. Soyopa, Loma Maderista, 3.5 km S of Tonichi, ca. 28°34′N, 109°33′W, *T. Van Devender & A. Reina G. 2001-184* (ARIZ, CAS); El Rancheria crossing of Río Cuchujaqui, ca. 22.5 km S of Alamos on road to El Chinal, 26°51′N, 108°55′W, *T. Van Devender et al. 92-1190* (ARIZ); near Tojibampo, 19.5 km NNW of San Bernardo toward Mesa Colorada, 27°02′N, 108°47′W, *T. Van Devender et al. 93-368* (ARIZ, CAS); Mpio. Navojoa, Teachive de Masiaca, 26°47′N, 109°14′W, *T. Van Devender et al. 95-105* (ARIZ); 1.5 km SW of Santa Ana on road to Guadallupe Tayopa, 28°23′N, 109°09.5′W, *T. Van Devender et al. 97-215* (MEXU); Mpio. Nogales, Sierra Las Avispas, 14.6 km W of MEX 15 on SON 43 (to Sáric), 31°07′N, 111°04`E, *T. Van Devender et al. 2002-745* (CAS); Palm Canyon, 17.7 mi SE of Magdalena in Cerro Cinta de Plata, *T. Van Devender et al. s.n.* (ARIZ); San Javier, cañón entre los cerros El Potrerito y Los Amoles, 7 km S del poblado, 28°32′N, 109°45′W, *L. Varela E. 96-309* (MEXU); San Javier, cerro El

Verde, 3 km de la carr. 16, 28°34′N, 109°44′W, *L. Varela E. 96-456* (MEXU); Puerto de Huépari, NW of Aribabi, *S. White 2773* (GH, MICH, US); Cañón de la Petaquilla (just W of Bavispe), *S. White 3333* (GH, MICH); Cañón del Agua Amarga (E of Oputo), *S. White 3612* (MICH); Horconcitos, Río Huachinera, *S. White 3727* (ARIZ, MICH, GH); Colonia Morelos, *S. White 4420* (MICH), *4455* (ARIZ, GH, MICH, NY, US); western foothills of Sierra de la Cabellera, ca. 10 mi E of Colonia Morelos, *S. White 4470* (ARIZ, GH, MICH, US); 4 mi N of Nuri, 28°10′N, 109°19′W, *A. Whittemore et al. 83-085* (CAS, TEX); 5 mi S of San Rafael, *I. Wiggins 5942* (DS, US); 2 mi E of Rancho San Carlos toward Norio, *I. Wiggins 6147* (DS, US); 1 mi W of jct. Cananea and Remedios roads on upper ford of Río Magdalena, *I. Wiggins 7096* (DS, MICH, US); Río Sásabe, 10 mi E of Magdalena, *I. Wiggins 7115* (DS, F, LL, MICH, UC, US); ca. 14 mi S of Divisaderos, *I. Wiggins 7466* (DS, MICH, US).

Tetramerium tenuissimum Rose, Contr. U.S. Natl. Herb 1:349. 1895. TYPE: MEXICO. Colima: vicinity of Colima, 27-28 Feb 1891, *E. Palmer 1297* (holotype: US!; isotypes: GH!, K!, NY!, US!).

Tetramerium leptocaule Happ, Ann. Missouri Bot. Gard. 24:516. 1937. TYPE: MEXICO. Michoacán: Distr. Huetamo, Tacupa, 17 Jan 1934, *G. Hinton et al. 5494* (holotype: K!; isotypes: DES!, GH!, MO!, NY!, US!).

Phenology. Flowering: September–March; fruiting: September–March.

Distribution and habitats. Mexico (Campeche, Chiapas, Chihuahua, Colima, Guanajuato, Guerrero, Jalisco, Michoacán, Morelos, Nayarit, Sinaloa, Sonora, Veracruz, Yucatán); Sonoran plants occur on slopes, along streams, and in disturbed areas in thornscrub and tropical deciduous forests at elevations from 200 to 920 m.

Illustration. None found.

Local names. "Rama del toro" (fide Van Devender et al. 2000); "rama toro" (*Gentry 1084*); "tau-i-we toro" (Guarijío, *Gentry 1084*).

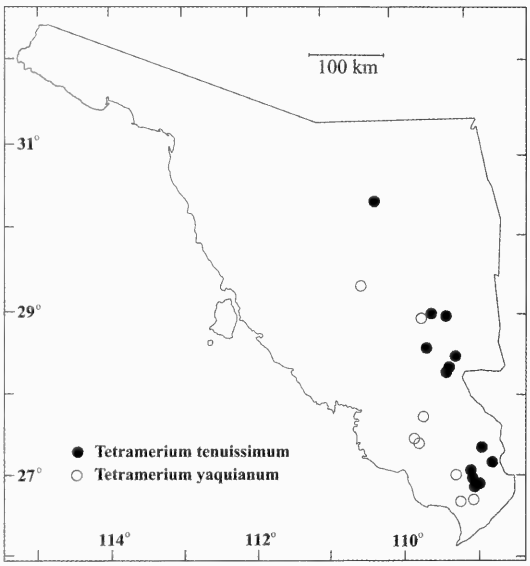

FIGURE 41. Sonoran distribution of *Tetramerium tenuissimum* and known distribution of *T. yaquianum*.

Daniel (1986, 1995a) and Daniel and Acosta (2003) provided descriptions of this species. Until recently, *Tetramerium tenuissimum* was thought to be quite rare. It is now being found in regions of dry forest throughout Mexico and Central America. It reaches the northern and western extents of its distribution in north-central Sonora (Fig. 41). Sonoran plants of *T. tenuissimum*, which often grow in close proximity to *T. nervosum* and which are often mistaken for it, can be distinguished from that species by the characters in the following couplet:

1. Calyx 4-lobed; margin of bracts conspicuously ciliate with at least some (usually most) trichomes 1–4 mm long; bracteal apex usually twisted. . . . . *T. nervosum*
1. Calyx 5-lobed; margin of bracts ± inconspicuously ciliate with trichomes 0.05–0.5 mm long; bracteal apex not twisted. . . . . *T. tenuissimum*

SONORAN COLLECTIONS: along road to El Tezal, 2.6 mi W of Alamos, *T. Daniel 3374* (CAS, ENCB, MEXU); *3384* (ASU, NY, US); Mpio. Yécora, along Hwy. 16, 2.6 km NW of Tepoca, ca. 28°27′N, 109°16′W,

T. Daniel et al. 8565 (CAS); Mpio. Yécora, between San Nicolás and Nuri, just S of Curea, ca. 24 km SW jct. Hwy. 16, ca. 28°19′W, 109°17′W, *T. Daniel et al. 8575* (CAS); Mpio. Yécora, Arroyo La Quema, 0.3 km SE of Tepoca on Hwy. 16, ca. 28°26′N, 109°15′W, *T. Daniel et al. 8637* (CAS, MEXU); Canyon Sapopa, Río Mayo, *H. Gentry 1084* (ARIZ, F, GH, MO); Río El Naranjo crossing N of Taymuco, 27°15′N, 108°43′W, *P. Jenkins et al. 88-320* (ARIZ, CAS); Mpio. Arizpe, Puente Caliente, Rancho Agua Caliente, ca. 3 km S of Arizpe on Son. 89, 30°20′N, 110°12′W, *A. Reina G. & T. Van Devender 2000-738* (ARIZ, CAS); Mpio. Yécora, Curea, 28°19′N, 109°17′W, *A. Reina G. et al. 2001-79* (CAS, MEXU, MO), *2001-80* (CAS); Mpio. Yécora, Arroyo Santa Ana at SON 12 (Tepoca-Cd. Obregón Hwy.), 2.3 km SW of La Quema turnoff, 8.5 km (air) W of Guadalupe Tayopa, 28°21′N, 109°16′W, *A. Reina G. et al. 2001-98* (CAS); Mpio. Alamos, Arroyo Mentidero at crossing of Alamos-El Chinal road and down arroyo to Río Cuchujaqui, ca. 12 km S of Alamos, ca. 26°55′N, 108°55′W, *A. Sanders et al. 12617* (CAS); Mpio. Yécora, Arroyo Santa Ana at Son. 12, 2.3 km SW of turn to La Quema, 28°21′N, 109°16′W, *T. Van Devender & A. Reina G. 97-1060* (ARIZ, CAS, MEXU); Mpio. Soyopa, Loma Maderista, 3.5 km S of Tónichi, ca. 28°34′N, 109°33′W, *T. Van Devender & A. Reina G. 2001-199* (CAS, MO); ca. 8 mi SE of Alamos near Río Cuchujaqui, *T. Van Devender & R. Van Devender 83-142* (ARIZ, CAS), *84-142* (ASU); *T. Van Devender et al. 84-153* (ASU); ca. 13.5 mi S of Alamos, *T. Van Devender et al. 84-191* (ASU); El Guayabo crossing of Río Cuchujaqui, 14 km ESE of Alamos, 27°00′N, 108°47′W, *T. Van Devender et al. 92-257* (ARIZ, CAS), *92-1291* (ARIZ, CAS, TEX); El Ranchería crossing of Río Cuchujaqui, ca. 22.5 km S of Alamos toward El Chinal, 26°51′N, 108°55′W, *T. Van Devender et al. 92-1192* (ARIZ, CAS, MO, TEX); Cerro las Tatemas below Microondas La Luna, 13.8 km NW of Alamos, 27°07′N, 109°02′W, *T. Van Devender et al. 93-338* (ARIZ, CAS); Sierra de Alamos, El Rincón Viejo, Arroyo El Aguaje, ca. 4 km N of Alamos, 27°04′N, 108°56′W, *T. Van Devender et al. 93-1507* (ARIZ, CAS); Mpio. Soyopa, NE side of Río Yaqui bridge on Mex. 16, just S of Tónichi, ca. 28°34′N, 109°33′W, *T. Van Devender et al. 97-1471* (CAS); Mpio. Bacanora, jct. of Cañada Jiropa on road from Bacanora to Tónichi, 5.4 km (air) SSW of Bacanora, 28°56′N, 109°25′W, *T. Van Devender et al. 99-861* (CAS, TEX); Mpio. Arivechi, Arroyo Agua Caliente, 10.2 km (air) WNW of Arivechi, 28°57′N, 109°17′W, *T. Van Devender et al. 99-886* (ARIZ, CAS); Mpio. Yécora, 1.9 km W of Tepoca on Mex. 16, 28°27′N, 109°16′W, *T. Van Devender et al. 2000-61* (CAS); Mpio. Yécora, Curea, 28°19′N, 109°17′W, *T. Van Devender et al. 2001-100* (CAS).

Tetramerium yaquianum T.F. Daniel, Syst. Bot. Monogr. 12:102. 1986. TYPE: MEXICO. Sonora: along rd. to Micro. Cerro Prieto, between Navojoa and Alamos, 9.7 mi E of jct. Hwy. 15 in Navojoa, 13 Mar 1984, *T. Daniel 3372* (holotype: CAS!; isotypes: ASU!, MEXU!, MICH!, NY!, US!).

Phenology. Flowering: July–December, March; fruiting: September–December, March.

Distribution and habitats. Endemic to Sonora where plants occur on slopes and along streams in thornscrub and tropical deciduous forests at elevations from 110–400 m.

Illustration. *Systematic Botany Monographs* 12:76. 1986.

Daniel (1986) provided a description of *Tetramerium yaquianum*. It is the only species of Acanthaceae known to be restricted in distribution to Sonora (Fig. 41), where it can be distinguished from the morphologically similar *T. nervosum* by the characters in the following couplet:

1. Calyx 5-lobed; bracts widely spreading (usually ± horizontal), glandular pubescent with glandular trichomes 0.2–0.3 mm long, (acute to) rounded to truncate to emarginate at apex, the apical portion usually flat and not twisted. . . . . *T. yaquianum*
1. Calyx 4-lobed; bracts mostly erect (± appressed to rachis), not glandular pubescent (or if glandular trichomes, if present, these up to 0.1 mm long), acute to acuminate at apex, the apical portion usually ± recurved and twisted. . . . . *T. nervosum*

Sonoran collections: between Ures and Hermosillo, 17.1 mi SW of Ures, *T. Daniel 940* (MICH); between Esperanza and Rosario de Tezopaco, 33.3 mi NE jct. Hwy. 15, *T. Daniel 3361* (ASU, CAS, MICH, MEXU, NY, US); western base of Sierra Bojihuacame, 1.2-1.1 mi SE of Bachoco, *T. Daniel 3365* (ASU, CAS,

ENCB, K, MEXU, MICH, NY, UC, US); El Novillo (E-central Sonora), *R. Felger et al. 84-298* (ARIZ); Sierra Bajihuacame, SE of Cd. Obregón, *H. Gentry 14530* (ARIZ, LL); summit of Cerro Prieto, 15 km E of Navojoa toward Alamos, ca. 27°15′N, 109°17′W, *A. Sanders et al. 9279* (CAS); 37 mi NE of Cajeme on road to Tesopaco, *F. Shreve 6158* (ARIZ, F); 1.5 mi downstream from La Estrella on Río Yaqui, *T. Van Devender et al. s.n.* (ARIZ, ASU); Mesa Masiaca along road to microwave tower, 6.5 km WNW of San José de Masiaca, 26°46′N, 109°18′W, *T. Van Devender et al. 92-1109* (ARIZ, CAS, MO, TEX); Mpio. Alamos, Cerro El Chorro, 4 km NW of Yocogigua, 26°49′N, 109°03′W, *T. Van Devender et al. 93-1445* (ARIZ, CAS).

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